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GENETICS

A Periodical Record of Investigations Bearing on Heredity and Variation

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A STUDY OF THE EFFECT OF X-RAY RADIATION ON OCCURRENCE OF ABNORMAL INDIVIDUALS, MUTATION RATE, VIABILITY AND FERTILITY OF THE PARASITIC WASP, *HABROBRACON JUGLANDIS* (ASHMEAD)

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Columbia University, New York City

Received December 6, 1930

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INTRODUCTION

The notable discovery by MULLER (1927) that genic mutations could be produced by X-ray radiations in Drosophila led the author to attempt to increase the number of segregating characters in *Habrobracon juglandis* (Ashmead) by the same method, and to study the effect of X-ray radiation on mutation rate, viability and fertility. The experiment was started in November, 1927, and the present publication is a report of the results.

ACKNOWLEDGMENTS

The author gratefully acknowledges indebtedness to Doctor P. W. WHITING at the UNIVERSITY OF PITTSBURGH for material; to the Faculty of Zoology of COLUMBIA UNIVERSITY and Doctor THOMAS HUNT MORGAN, now at the CALIFORNIA INSTITUTE OF TECHNOLOGY, for approval of, and helpful suggestions concerning the problem chosen for investigation; to Doctor JOHN W. GOWEN, ROCKEFELLER INSTITUTE FOR MEDICAL RESEARCH, for suggestions and criticisms; to the Director and Staff of the CROCKER INSTITUTE OF CANCER RESEARCH for the use of space and equipment; and to the NATIONAL RESEARCH COUNCIL, Committee on the Effect of Radiation upon Living Organisms, for financial aid.

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MATERIAL AND METHODS

The material used consisted of two wild-type strains of Habrobracon, one derived from Lancaster and the other from Iowa City stock, two mutant allelomorphic eye-color stocks, and one mutant reduced wing stock. The eye colors were orange, a recessive to black or type (WHITING 1921), and ivory recessive to type and orange (WHITING and BURTON 1926). The mutant stock reduced wing was a single factor recessive to normal wing (WHITING 1926a).

At the beginning of the experiment the females which were treated were heterozygous for two allelomorphs for eye-color and for normal and reduced wing. That is, the females radiated were either black-eyed normal carrying orange or ivory with reduced wing, or orange-eyed normal heterozygous for ivory and reduced wing. The control females were likewise heterozygous for orange or ivory eye-color and reduced wing. Two independent recessive characters, bar and eyeless, which will be discussed later, arose during the course of the experiment and were added to the genetic constitution of the treated and control females.

The age at which the individuals were treated varied from mature or nearly mature eggs in the body of the adult through all stages of larval development. After the exposure to X-ray the larvae were returned to their vials and allowed to mature at 30 degrees C. The hatched females were observed and allowed to breed as virgins or mated to their recessive brothers and bred. Their progeny were then observed and the females again mated with their recessive brothers or allowed to breed as virgins. This procedure was continued for several generations. The treated adult females were allowed to breed as virgins and their haploid sons were observed for mutations. In the latter case the treatment was effective during the last miotic division of the egg or on the mature egg prior to laying, while in the former it is the egg after it has been laid or the larva during its early development which is exposed to the treatment. The data thus far accumulated are insufficient to show the relationship between the age at which the individual is treated and the appearance of the mutation, and will not be discussed in the present publication.

The X-ray machine used was a Wappler Diex equipped with a Coolidge tube and tungsten target. No metallic filters were used. The efficiency of the machine was repeatedly checked with physical and biological tests by Doctor CHARLES PACKARD. The intensity of the dose varied from 1200 to 8000 Roentgen units in the different experiments.

THE EFFECT OF X-RAY RADIATION ON OCCURRENCE OF ABNORMAL INDIVIDUALS AND MUTATION RATE

The effect of X-ray radiation on the increase in the proportion of individuals in a given population showing somatic abnormalities is presented briefly in table 1. The first four columns show the number of fertile matings, the number of their progeny, the number and percentage of indi-

TABLE 1

The effect of X-ray radiation on the occurrence of abnormal individuals in the directly X-rayed, 1, 2, 3 and later generations from the treatment.

GROUP	NUMBER OF FERTILE MATINGS	TOTAL NUMBER OF PROGENY	NUMBER OF ABNORMALITIES	PERCENT OF ABNORMALITIES	DIFFERENCE FROM CONTROL IN PERCENT ABNORMAL ± THE P.E.	DIFFERENCE ÷ P.E. DIFFERENCE	PERCENT TREATED ABNORMAL ÷ PERCENT CONTROLS ABNORMAL
Controls	928	21504	29	0.135	..	..	..
Directly X-rayed	329	3748	64	1.708	1.573±0.072	21.83	12.65
Generation 1 from X-ray	640	10098	92	0.911	0.776±0.050	15.52	6.75
Generation 2 from X-ray	438	7239	63	0.870	0.735±0.052	14.13	6.44
Generation 3 from X-ray	288	4588	39	0.850	0.715±0.056	12.77	6.30
X-rayed stock	1398	19068	118	0.619	0.484±0.040	12.10	4.59
Total X-rayed	3093	44741	376	0.840	0.705±0.044	16.02	6.22

viduals with somatic abnormalities in the control group, among the directly X-rayed individuals, and the first, second, third and later generations of their descendants. The fifth column represents the difference in the percentage of abnormal individuals between the control and the treated groups with its probable error. The probable error of the difference in the percentages was calculated by the formula:

$$\text{P. E. of } 100p_1 - 100p_2 = 100 \times 0.67449 \times \text{standard error } p_1 - p_2$$
$$= 100 \times 0.67449 \sqrt{p_0 q_0 (1/n_1 + 1/n_2)}$$

where in each case n_2 is the number of individuals in the control group while n_1 is the number of individuals in the group designated in the corresponding line of the table. Similarly p_2 is equal to the proportion of somatic abnormalities in the control group and p_1 the proportion in the respective treated group. The proportions of abnormal and of normal individuals in the progeny of the control and the compared treated group combined are designated respectively by p_0 and q_0. That is, the standard error

of the difference between the two proportions calculated by the method clearly described by YULE (1922) was reduced to the probable error of the difference between the two proportions by multiplying by the constant 0.67449 and was then converted to a percentage basis by multiplying by 100.

The sixth column shows the ratio of the difference between the percentage of abnormalities in each treated group and the control group to the probable error of this difference. This ratio can be considered as a measure of the statistical significance of the difference. PEARL and MINER (1914) prepared from the probability integral tables a table showing for this ratio the expectation in 100 trials of a deviation as great or greater than the one observed if the sole difference between the compared groups was due to sampling. Their table also shows the odds against the observed result being due to pure random sampling chance. This table slightly enlarged by PEARL (1923) extends from Deviation ÷ P. E. Deviation = 1, the point where a deviation as great or greater than the one observed is as likely as not to be due to fluctuations in sampling, to Deviation ÷ P. E. Deviation = 10, where the odds against the observed deviation being due to random sampling are 65,000,000 to 1. The ratios (percent abnormal treated − percent abnormal controls) ÷ (P. E. percent abnormal treated − percent abnormal controls) shown in column six of table 1 vary from 12.10 to 21.83 and therefore the odds against any of the observed differences in proportion of abnormalities in the control and treated groups being due to chance is overwhelming. The final column of the table shows the number of times that the percentage of somatic abnormalities in the treated exceeded the percentage of abnormalities in the controls. The calculations for the table were made to six decimal places and then tabulated to three.

The controls for the experiment consisted of 1023 matings made up from the same stocks with females of the same age and carrying the same genetic characters as the treated individuals. Of these 302 were completed at the time the experiment started and 721 were made up as sister matings and bred contemporaneously with the treated individuals. There were 95 sterile matings and 928 fertile matings which produced 13,787 males, 7,540 females and 5 gynandromorphs or a total of 21,504 progeny. As seen in the first line of table 1 there were 29 or 0.13 percent of abnormal individuals among the 21,504 individuals. The abnormalities were classified as such on the basis of their somatic appearance and those tabulated in the control and treated groups of tables 1 and 2 include all the changes in visible characters which were observed. From the nature of the experiment it is obvious that only certain types of mutations would be detected, that

is, only mutations which were expressed by the third allelomorph among the sons and daughters of females heterozygous for two allelomorphs at the orange eye color locus unless they occurred in mosaic patterns, and at the reduced locus, only the mutations which were expressed as mosaics or affected enough of the germ cells to cause a significant deviation from the expected 1 to 1 ratio, would be observed. The males would show all the new mutations which occurred since they are haploid, but the females would only express the new dominant mutations. This applies equally to the controls and treated groups, and the majority of observed abnormalities were mosaic individuals. Lethal mutations were not observed. This is not

TABLE 2

Showing the comparison between ♂♂ and ♀♀ in percentage of abnormal individuals.

GROUP	TOTAL NUMBER ♂	TOTAL NUMBER ♀	NO. ♂♂ ABNORMAL	NO. ♀♀ ABNORMAL	PERCENT ABNORMAL ♂♂	PERCENT ABNORMAL ♀♀	PERCENT ABNORMAL ♂♂ −PERCENT ABNORMAL ♀♀ ± P.E.	DEVIATION ÷ P.E. DEV.
Controls	13787	7540	15	9	0.11	0.12	−0.01±0.03	0.3
Directly X-rayed	2371	1374	37	24	1.56	1.75	−0.19±0.18	1.0
Generation 1	7838	2258	70	20	0.89	0.88	0.01±0.15	0.7
Generation 2	4808	2431	46	17	0.96	0.70	0.26±0.16	1.6
Generation 3	3255	1329	25	10	0.77	0.75	0.02±0.19	0.1
X-rayed stock	12840	6218	80	28	0.62	0.45	0.17±0.08	2.1
Total X-rayed	31112	13610	258	99	0.83	0.73	0.10±0.06	1.7

surprising since the males are haploid and any bearing lethals would not appear and in females lethals could only be detected in chromosomes which are marked by visible characters. The possibility of discovering lethal changes when only a small number of visible characters are known is slight, and the failure to demonstrate them does not prove that none had occurred.

Individuals from 378 matings were exposed to X-ray radiation, but progeny from only 329 survived. From the 329 fertile matings 2371 males and 1374 females and 3 gynandromorphs or a total of 3748 individuals were hatched. The second line of table 1 shows that of 3748 directly X-rayed individuals 64 or 1.71 percent showed changes in visible characters. Of the 64 abnormal individuals, 37 were males, 24 females and 3 sex mosaics. Disregarding the sex mosaics table 2 shows that the 37 abnormal males occurred among 2371 males or 1.57 percent were abnormal. The 24 abnormal females were equal to 1.75 percent of 1374 females. Of the 29 abnormal individuals in the controls 15 were males, 9 were females and 5 were sex

mosaics. That is, 0.11 percent of the 13,787 males and 0.12 percent of the 7,540 females showed somatic abnormalities. The ratio of the percentage of abnormalities of treated males to that of the control males is 14.46 and of the treated to the control females it is 14.63, or the individuals with somatic abnormalities are equally represented in the male and female population. The difference between the percentage of abnormalities in the totals of the treated and controls was 1.57 ± 0.072 percent which is 21.8 times its probable error. The last figure in the second line of the table shows that the percentage of somatic abnormalities among the directly X-rayed individuals was 12.6 times that of the controls.

That we might at the beginning rule out the possibility that the increased proportion of somatic abnormalities among the X-rayed individuals was due in part to the selection or inclusion of individuals which had an hereditary tendency to produce deficient or abnormal progeny such as the case of deficiency in the posterior part of the digestive tract described by WHITING (1926b), a series of 96 matings was made up and the progeny in each culture while still in the larval stage were divided into two nearly equal groups, one of which was X-rayed and the other allowed to hatch as controls. The result from these divided matings will be found in table 3. From the 96 matings, 1992 progeny including 25 individuals showing

TABLE 3

The effect of X-ray radiation on proportion of abnormal individuals where one-half the individuals from each mating were treated and the other half were the controls.

DIVIDED MATINGS	NUMBER OF ½ MATINGS	TOTAL PROGENY	NUMBER OF ABNORMALITIES	PERCENT ABNORMAL	DIFFERENCE BETWEEN TREATED AND CONTROL ± P.E.	DIFFERENCE ÷ P.E. DIFFERENCE	PERCENT TREATED ABNORMAL ÷ PERCENT CONTROLS ABNORMAL
X-rayed ½	96	924	24	2.597	2.503 ± 0.337	7.43	27.74
Control ½	96	1068	1	0.094	..	..	..
Total	96	1992	25	1.255	..	..	..

somatic abnormalities were hatched. Of these 1992 progeny 1070 were males and 922 females and of the 25 abnormal individuals 13 were observed as males and 12 as females. The first line of the table shows that 924 of these were X-rayed and among them 24 or 2.60 percent somatic abnormalities were observed while in the 1068 individuals of the non-radiated half there was only 1 or 0.09 percent of abnormal individuals. The difference between the percentage of abnormal individuals in the X-rayed half

and the non-treated half of the same matings is 2.50 ± 0.34 percent or 7.43 times its probable error, which means that the expectation of a deviation as great or greater than this if the two groups were random samples of the same population would be 0.0001363 in 100 trials or that the odds against the two being independent random samples of the same population are 642,200 to 1.[1] The final column of the table shows that the percentage of abnormalities among the X-rayed individuals was 27.7 times that of the non-treated half. The fact that the increase in proportion of abnormalities over the controls is greater here than in the group shown in table 1 may in part be due to the selection of dosage used and the age at which the individuals were treated. However, the occurrence of a difference so certainly significant here where all the possibility of a genetic factor difference is ruled out demonstrated beyond any reasonable doubt that it was the treatment that was the effective agent in producing the increased percentage of abnormal individuals. The abnormal individuals recorded here represent quite fairly on a small scale the types of abnormalities observed in the larger group of the directly X-rayed individuals and their descendants. There were 2 black and orange eye-color mosaics, 1 male and 1 female, 4 males and 3 females with defective median veins in the primary wings, 6 males and 7 females with vestigial wings and one of these males was the one observed abnormal individual in the control half, 1 male with fused antennae, 1 male with abnormal head possibly eyeless and 1 female with abnormal abdomen. The progeny from these matings are included in the later generations of the treated individuals and in the controls.

It appears from an examination of tables 1 and 2 that the descendants, male and female, for three successive generations, of the individuals exposed to X-ray and the "X-rayed stock" which includes the fourth generation from the treatment, and all the later generations which were sufficiently tested to be considered showed a significantly higher proportion of abnormal individuals than did the controls. There were 6 times as many individuals with somatic abnormalities in the first, second and third generations of descendants and 4 times as many in the X-rayed stock as there were in the controls.

The occurrence of a substantially increased proportion of abnormal individuals among the progeny of those exposed to X-ray two, three and more generations after the treatment was unexpected and cannot at present be explained. It is quite possible that some of the so called abnormal in-

[1] These values were obtained from PEARL and MINER's table by interpolation. From the probability integral table, the expectation in 1000 is $p = 0.000,000,556$. The odds are 1,798,560 to 1.

dividuals are the result of non-inherited developmental irregularities such as "shot" described by WHITING (1930), and that their occurrence in later generations is a result of some fundamental injury to the germ-plasm. Some of the mosaic females may have resulted from chromosome deletion or translocations such as those described by MULLER (1928) in Drosophila. Some without doubt represent somatic and germinal mutations, but why they should repeatedly occur two, three and more generations after the treatment is not known. However, in the following tables, 4 to 7 inclusive, are tabulated those abnormal individuals which morphologically resembled a change at the orange-ivory eye-color, reduced wing, bar and eyeless loci, and in the text which accompanies the discussion of each table will be represented the evidence for considering some of them as genic mutations.

Table 4 shows briefly that there were 49 individuals in the experiment which somatically resembled mutations in one of the three known allelo-

TABLE 4

Showing the effect of X-rays on the production of eye-color mutations at the orange locus in the directly X-rayed 1, 2, 3 and later generations from the treatment.

GROUP	NUMBER OF FERTILE MATINGS	TOTAL NUMBER OF PROGENY	NUMBER OF EYE-COLOR MUTATIONS	PERCENT OF EYE-COLOR MUTATIONS	DIFFERENCE FROM CONTROLS IN PERCENT EYE-COLOR MUTATIONS ± P. E.	DIFFERENCE ÷ P.E. DIFFERENCE
Controls	928	21504	1	0.005	..	..
Directly X-rayed	329	3748	7	0.187	0.182±0.021	8.67
Generation 1 from X-ray	640	10098	14	0.139	0.134±0.018	7.44
Generation 2 from X-ray	438	7239	10	0.138	0.133±0.018	7.39
Generation 3 from X-ray	288	4588	3	0.065	0.060±0.014	4.29
X-ray stock	1398	19068	14	0.073	0.068±0.013	5.23
Total X-rayed	3093	44741	48	0.107	0.102±0.015	6.80

morphs for eye-color (that is, orange, ivory and their normal allelomorph black or type). One of these occurred in the controls and 48 in the radiated individuals and their descendants. The directly X-rayed individuals showed an increased percentage of 0.182 ± 0.021 or a difference from the controls which is 8.67 times its probable error. The first and second generations showed a correspondingly significant increase over the controls or a difference 7 times as great as its probable error. Among the third and later generations of descendants the difference is also significant, that is, respectively 4 and 5 times its probable error.

The mutant individuals recorded in table 4 consist of 2 black-eyed sons from orange-ivory heterozygous mothers mated to ivory males, 9 orange

sons from black-ivory heterozygous mothers, 4 ivory sons from black-orange heterozygous mothers, 23 black and orange mosaic individuals from black and ivory heterozygous females mated to ivory males or bred as virgins, 7 black and orange mosaics from black and orange heterozygous females mated to ivory males or bred as virgins, 2 black and ivory mosaic females from ivory females mated to black males, and 2 orange and ivory mosaic sons from orange and ivory heterozygous females.

It is impossible to say whether the 7 black and orange mosaics from black and orange heterozygous females, and the 2 orange and ivory mosaic sons from orange-ivory heterozygous mothers were genic mutations or arose from binucleate eggs. That is, the female parent in each case was heterozygous for the two colors represented in the eyes of the mosaic. However, these female parents were also heterozygous for reduced and normal wing but in no case did the eye-color mosaics have mosaic wings.

The two black and ivory mosaic females from ivory females mated to black reduced males may represent genic mutations or abnormal fertilization. One of these females produced both black and ivory sons and the other was sterile. The two black males from orange-ivory heterozygous females mated to ivory males, and the four ivory males from black-orange heterozygous virgin females could not have resulted from either abnormal fertilization or binucleate eggs.

The 9 orange, and 23 black and orange mosaic individuals from black-ivory heterozygous females express a color, orange, which was not present in the germ-plasm of the parents. These mosaics appear to be quite similar to those previously described by WHITING (1927). The amount of each color represented varied from individuals with one eye orange and the other black (figure 1), or individuals with orange eyes each containing black sectors (figure 2) or bars, to individuals with the orange eye-color represented only by a few ommatidia or the ocelli (figure 3). There were also 4 individuals which phenotypically expressed all three allelomorphs (figures 4 and 5). The ratio of mutant to non-mutant color in the eyes bore no direct relation to the behavior of the germ-plasm.

WHITING (1928b) suggested that the occasional occurrence of black-orange mosaic sons from black-ivory heterozygous mothers might be due to an orange appearance in a black-ivory mosaic caused by the proximity of the black and ivory facets. If these mosaics are truly black and ivory and not black and orange they may have arisen either as genic mutations or from binucleate eggs. There is no evidence that any of these were black-ivory mosaics but there is proof that several of them were not. Three of the orange mutants were tested and 2 proved to be genetically orange; the

LEGEND FOR PLATE 1

Magnifications are × 20 for figures 1–8 inclusive, × 15 for figures 9–15 inclusive.

FIGURES 1–3.—Dorsal view of head of eye-color mosaics showing distribution of black and orange color. (Mosaics $192A_1$, $4463A_1$, $5289A_1$.)

FIGURES 4, 5.—Dorsal and sinistral view of tri-color mosaic showing distribution of black, orange and ivory color. (Mosaic $1195A_1$.)

FIGURES 6, 7.—Dorsal and sinistral view of head of a bar-eyed male.

FIGURE 8.—Dorsal view of head of an eyeless male.

FIGURE 9.—Normal right primary wing.

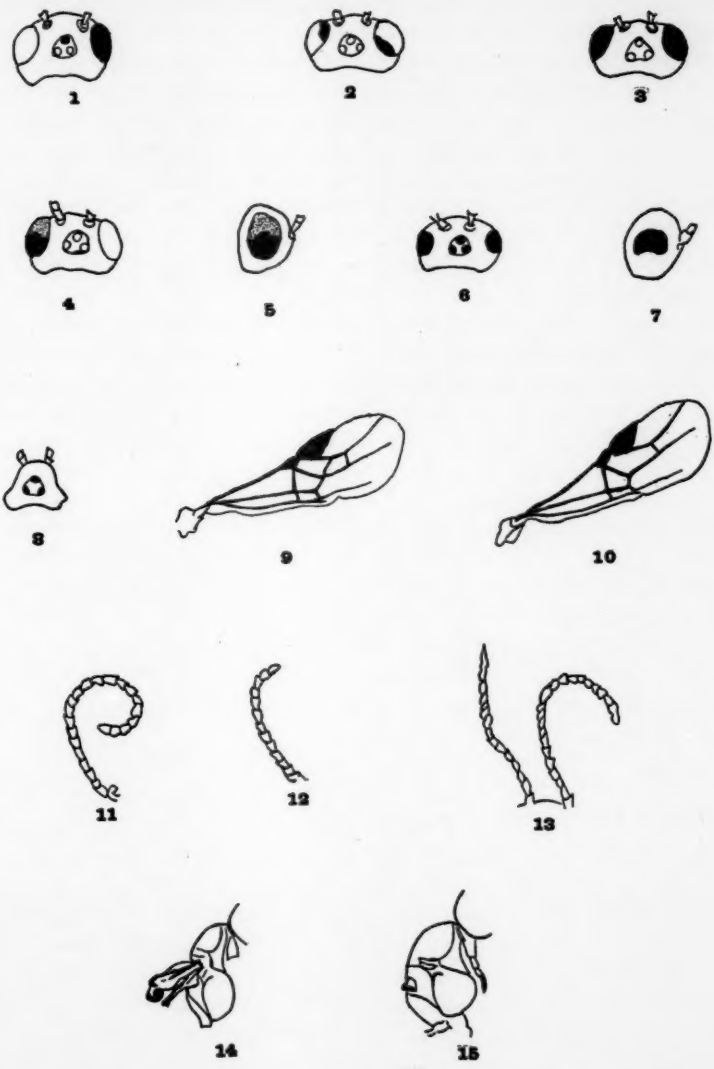
FIGURE 10.—Defective wing showing the absence of a part of the median vein.

FIGURES 11, 12.—Normal right male and female antenna.

FIGURE 13.—Antennae of a fused antennal male.

FIGURE 14.—Dextral view of thorax showing vestigial wing.

FIGURE 15.—Dextral view of thorax of wingless male.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other bred as black and might therefore have been a black-ivory mosaic, but both of its eyes were orange and did not show any black tissue. Seven of the black-orange mosaics were tested, 4 bred as black, 1 as orange and 2 as black and orange. Since five of the orange mutants, 2 orange, and 3 mosaics of orange, proved to be genetically orange and none proved to be ivory, we are not justified in considering those which did not breed as orange as black-ivory mosaics. Furthermore, the female parent was in each case heterozygous for reduced and non-reduced wing, and it would be expected that if these mosaics arose as a result of the fusion of an ivory and a black bearing nucleus thereby making them black-ivory mosaics, that some of them would also be mosaic for reduced and normal wing, but this was not the case.

WHITING (1928b) also suggests a "genetic" hypothesis which might account for the occurrence of orange eye-color among the progeny of the black-ivory heterozygous females. That is, ivory may be caused to mutate to orange in association with black. The evidence relating to this hypothesis is not very satisfactory. But if ivory is more likely to mutate to orange in association with black than with orange or shows a higher mutation rate than the orange and black allelomorphs, the progeny of the black-ivory heterozygous females in the treated group should be compared separately with the progeny of the black-ivory heterozygous females in the control group. When this is done, it appears that the only mutation observed in the control group was a black-orange mosaic from a black-ivory heterozygous female. In the control group there were 127 black-ivory heterozygous females which produced 1969 progeny including 1 or 0.05 percent of orange mutants. This mosaic was sterile. There were 60 matings in the directly X-rayed group with 706 progeny including 3 or 0.42 percent of orange individuals. The difference is 0.37 ± 0.11 percent or a difference 3.3 times its probable error. Generation 1 included 264 fertile black-ivory heterozygous females which produced 4172 progeny with 8 or 0.19 percent of orange mutants. The difference in this case is 0.14 ± 0.07 percent or 2.0 times its probable error. In generation 2 there were 146 black-ivory matings with 2438 progeny including 9 or 0.37 percent of orange individuals. This difference or 0.32 ± 0.10 percent is 3.2 times its probable error. In generation 3 there were 115 black-ivory females with 1913 progeny and 2 or 0.11 percent of orange mutants and in the X-rayed stock 9 or 0.17 percent among 5387 progeny. In neither of these cases was the difference statistically significant although the percent of orange mutants in the treated was 2 and 3 times respectively that in the controls.

When the progeny of the black-ivory heterozygous females in the treated group are compared separately with the progeny of the black-ivory females in the control group as is shown above, the increased percentage of orange mosaics is statistically significant for the directly X-rayed and for the second generation of descendants. The first, third, and later generations all show an increase in the same direction which is not statistically significant. This is the most vigorous selection of a control group since it includes the only mutation observed in untreated material in the smallest possible group. The decrease in the number of progeny in this selected control increases the percentage which the one observed mutation makes and at the same time increases the size of the probable error of difference. Yet it is conceivable that ivory is more likely to mutate in association with black than either of the other two allelomorphs in any combination, and that the apparent increase in eye-color mosaics among the treated individuals is due to a disproportionate percentage of these black-ivory heterozygous females in the treated and control groups. If this were the case when the progeny of such females are eliminated from both treated and controls, we would not expect a significant difference in the percentage of mutations in the two groups. In the treated group of 21,831 individuals not derived from black-ivory heterozygous females 18 or 0.082 percent showed changes in eye-color. There were no eye-color mutants among the 19,534 control individuals descended from black-orange and orange-ivory females. The difference between zero in the control and 0.082 ± 0.14 percent in the treated group is 6.0 times the probable error of the difference and therefore certainly significant. If we consider as mutations only the 2 black males from orange-ivory heterozygous females mated to ivory males, the 4 ivory males from black-orange heterozygous virgin females, the 2 orange and 3 black and orange mosaic individuals from black and ivory heterozygous mothers which were fertile and produced offspring showing the mutant eye-color, and compare them with the progeny of the black-orange, black-ivory and orange-ivory females in the control group, the increase in percent of mutations among the treated and their descendants is 0.034 ± 0.017 percent or only twice its probable error. There were also 6 sterile orange males and 17 sterile black and orange mosaics from black-ivory heterozygous females. It is of course quite impossible to prove that they were mutations, but the fact that they were sterile does not constitute evidence for or against an assumption that they were mutations. The 1 orange male and 3 black and orange mosaics from black-ivory heterozygous females which bred as black may have been so-

matic mutations to orange which failed to affect the germ-plasm or affected such a small fraction of it that it was not represented in their progeny.

In table 5 are included those individuals which morphologically resembled changes at the "reduced" locus. There were 3 in the controls and 3 among the directly X-rayed which gave an increase in the treated of

TABLE 5

Showing the effect of X-rays on the production of reduced wing mutations in directly X-rayed 1, 2, 3 and later generations from the treatment.

GROUP	NUMBER OF FERTILE MATINGS	TOTAL NUMBER OF PROGENY	NUMBER OF REDUCED WING MUTATIONS	PERCENT OF REDUCED WING MUTATIONS	DIFFERENCE FROM CONTROLS IN PERCENT OF REDUCED WING MUTATIONS ± P. E.	DIFFERENCE ÷ P. E. DIFFERENCE
Controls	928	21504	3	0.014	..	..
Directly X-rayed	329	3748	3	0.080	0.066±0.018	3.67
Generation 1 from X-ray	640	10098	0	0	−0.014±0.008	1.75
Generation 2 from X-ray	438	7239	0	0	−0.014±0.009	1.56
Generation 3 from X-ray	288	4588	0	0	−0.014±0.012	1.17
X-rayed stock	1398	19068	2	0.010	−0.003±0.007	0.43
Total X-rayed	3093	44741	5	0.011	−0.003±0.006	0.50

0.066± 0.018 percent or an increase 3.67 times its probable error. There were none in the first, second, or third generation of descendants and only 2 occurred among the X-rayed stock. In the total X-rayed group there were 5 or 0.01 percent of reduced wing mosaics with a difference from the controls of −0.003± 0.01 percent or an insignificant difference in favor of the controls. The failure to show a higher proportion of individuals resembling reduced mutations among the descendants of the treated group is probably influenced by the fact that only obvious mosaics could be detected. Since all of the females would produce both reduced and normal sons and daughters mutations affecting the entire individual or producing only small patches of the mutant tissue would not be easily observed.

Table 6 shows the effect of X-ray radiation on the occurrence of bar-eye (figures 6 and 7) mutations. This character is represented in the controls by one mosaic male in which one eye resembled the character as it occurred among the treated individuals. This control mosaic was sterile. Of the 29 which occurred among the progeny of the treated and their descendants, 17 showed the character in both eyes and 12 were mosaics. Eight of the first group were tested and 7 or 87.5 percent proved to be genetically bar. Six of the mosaics were tested and only 1 or 16.7 percent bred as bar. The occurrence of mutations at this locus in contrast to the reduced shows an insignificant difference between the controls and directly X-rayed indi-

viduals, but the first, second, third and later generations all show a significant increase over the controls.

The control and treated females represented in this table were not all heterozygous for the bar gene. The females therefore could not all have

TABLE 6

Showing the effect of X-rays on the production of bar eye mutations in the directly X-rayed, 1, 2, 3 and later generations from the treatment.

GROUP	NUMBER OF FERTILE MATINGS	TOTAL NUMBER OF PROGENY	NUMBER OF BAR-EYE MUTATIONS	PERCENT OF BAR-EYE MUTATIONS	DIFFERENCE FROM CONTROLS IN PERCENT OF BAR-EYE MUTATIONS ± P. E.	DIFFERENCE ÷ P. E. DIFFERENCE
Controls	928	21504	1	0.005	..	..
Directly X-rayed	329	3748	1	0.027	0.022±0.011	2.00
Generation 1 from X-ray	640	10098	7	0.069	0.064±0.013	4.92
Generation 2 from X-ray	438	7239	10	0.138	0.133±0.018	7.39
Generation 3 from X-ray	288	4588	3	0.065	0.060±0.014	4.29
X-rayed stock	1398	19068	8	0.042	0.037±0.010	3.70
Total X-rayed	3093	44741	29	0.065	0.060±0.012	5.00

shown the mutation had it occurred. If we consider only the male progeny from pure non-bar females of non-bar stock which have never been mated with bar stock, the percentage of bar mutation among them could not have arisen either from binucleate eggs or any form of chromosome duplication

TABLE 7

Showing the effect of X-rays on the production of eyeless mutations in the directly X-rayed, 1, 2, 3 and later generations from the treatment.

GROUP	NUMBER OF FERTILE MATINGS	TOTAL NUMBER OF PROGENY	NUMBER OF EYELESS MUTATIONS	PERCENT OF EYELESS MUTATIONS	DIFFERENCE FROM CONTROLS IN PERCENT EYELESS MUTATIONS ± P. E.	DIFFERENCE ÷ P. E. DIFFERENCE
Controls	928	21504	0	0	..	..
Directly X-rayed	329	3748	1	0.027	0.027±0.008	3.38
Generation 1 from X-ray	640	10098	1	0.010	0.010±0.005	2.00
Generation 2 from X-ray	438	7239	1	0.014	0.014±0.005	2.80
Generation 3 from X-ray	288	4588	0	0	..	..
X-rayed stock	1398	19068	8	0.042	0.042±0.009	4.67
Total X-rayed	3093	44741	11	0.025	0.025±0.007	3.57

There were 8 mosaics, 7 females and 1 male which occurred among the progeny of the females heterozygous for the bar gene. The seven mosaic females since they were heterozygous for bar and non-bar may owe their appearance to either the loss of the non-bar chromosome on one side of the

individual, partial fertilization, or to a somatic mutation from the normal gene to bar, but it would be impossible to discover which was the case without a cytological examination. The one male mosaic from a heterozygous bar mother may have arisen either as a somatic mutation or from a binucleate egg. There were 21 male bar mutants from pure non-bar females; 8 of these were tested and 7 or 87.59 percent behaved as true genic mutations; the other a mosaic of bar and normal bred as normal, as might be expected if the mutation had not affected the germ-plasm or only a small part of it. The remaining 13 were sterile. The one or 0.008 percent of bar mutants observed for the control group occurred among the 13,208 males from 871 pure non-bar females. One bar mutant among 2,145 directly X-rayed males from 298 non-bar females increased the percentage by 0.039 ± 0.017 percent. In generation 1, 7381 males including 3 or 0.41 percent of bar mutations were derived from 586 pure non-bar females. The difference in percent of bar mutations is 0.033 ± 0.014 or 2.5 times its probable error. The 405 pure non-bar females of the second generation produced 9 or 0.20 percent of bar mutants among their 4,396 sons. The difference in this case is 0.197 ± 0.028 percent or 7.0 times its probable error. In generation 3, 2 bar mutants occurred among 2,920 males from 246 pure non-bar females giving an increase over the controls of 0.061 ± 0.018 percent of bar mutants or an increase 3.2 times its probable error. The X-rayed stock likewise shows an increase of 0.061 ± 0.017 percent of bar mutants which is a significant increase over the controls. The 21 male bar mutants among the 25,600 sons of pure non-bar females in the sum of the treated individuals and their descendants show an increase over the controls of 0.074 ± 0.017 percent or an increase 4.4 times its probable error. If we consider as mutations only the 7 bar individuals which were fertile and bred as bar, the increased percentage over the controls is 0.027 ± 0.010 percent or 2.7 times its probable error. However, the character appeared the same in the sterile males as it did in the fertile ones, and that the former as well as the latter were genic mutations is obviously quite possible.

Table 8 shows the independent segregation of bar with three known independent characters, namely, black and orange eye-color, defective and non-defective wing venation, a factor for the presence or absence of vein r_4 (WHITING 1924) and reduced and normal wing. From 203 F_1 females from black bar males crossed with orange-eyed normal females, 433 black-eyed bar and 484 orange-eyed bar sons were obtained. Among the normal-eyed sons 49.5 percent were black and 50.4 percent orange. The deviation in the former case from the expected 50 percent is 2.78 ± 1.11 percent or not statistically significant. Thus eye-color is seen to segregate independently

with bar eye, but here bar is seen to lose out in competition with non-bar for as many bar as normal sons would be expected from these females.

The following two lines of the table show the progeny of 35 F_1 females from defective bar-eyed males crossed to normal females. There were 288 double dominant, 295 defective non-bar, 158 bar-eyed non-defective and

TABLE 8

Showing the independent segregation of the factor for bar eye and other known factors.

CHARACTERS TESTED	NUMBER OF HETEROZYGOUS F_1 ♀♀	TOTAL PROGENY	NUMBER DOMINANTS	NUMBER RECESSIVES	PERCENT DOMINANTS	PERCENT RECESSIVES	DEVIATION FROM EXPECTED 50 PERCENT ± P. E. DEV.	DEVIATION ÷ P. E. DEV.
Non-bar eye and eye-color	203	1467	727	740	49.557	50.443	0.443±0.881	0.50
Bar eye and eye-color	203	917	433	484	47.219	52.781	2.781±1.114	2.50
Non-bar eye and wing venation	35	583	288	295	49.400	50.600	0.600±1.397	0.43
Bar eye and wing venation	35	346	158	188	45.665	54.335	4.335±1.813	2.39
Non-bar eye and reduced wing	34	224	124	100	55.357	44.643	5.357±2.253	2.38
Bar eye and reduced wing	34	158	93	65	58.861	41.139	8.861±2.683	3.30
Non-bar eye and eyeless	32	202	132	70	65.347	34.653	15.347±2.373	6.47
Bar eye and eyeless	32	86	86	0	100.000	0	50.000±3.637	13.75
Non-bar eye and bar eye	518	4759	2939	1820	61.757	38.243	11.757±0.489	24.04

188 bar-eyed defective sons. Non-defective appears in 45.66 percent of the bar-eyed males and defective appears in 54.34 percent. The deviation from the expected 50 percent is 4.34±1.81 percent or less than three times its probable error, and bar can be said to assort independently of the factor for the defect in r_4 vein of the wing.

The fifth and sixth lines of table 8 show the segregation of the bar-eye factor with the factor for reduced wing. From 34 F_1 females heterozygous for bar and non-bar and reduced and normal wing, 124 normal eye non-reduced, 100 normal eye reduced, 93 bar-eye, normal and 65 bar-eye reduced sons were obtained. Reduced wing appeared in 41.14 percent of the bar-eyed sons with a deviation from the expected 50 percent of 8.86±2.68 percent which appears to be significant. However, this difference is probably due to the failure of some of the reduced wing individuals to come

through and not to any linkage between bar and reduced. The last line of table 9 shows the progeny from 110 females heterozygous for reduced and

TABLE 9

Showing the independent segregation of the factor for eyeless and other known factors.

CHARACTERS TESTED	NUMBER OF HETEROZYGOUS F_1 ♀♀	TOTAL PROGENY	NUMBER DOMINANTS	NUMBER RECESSIVES	PERCENT DOMINANTS	PERCENT RECESSIVES	DEVIATION FROM EXPECTED 50 PERCENT ± P. E. DEV.	DEVIATION ÷ P. E. DEV.
Normal eye and eye-color	110	991	502	489	50.656	49.344	0.656±1.071	0.61
Eyeless and eye-color	110	397	206	191	51.889	48.111	1.889±1.693	1.12
Normal eye, and wing venation	65	664	327	337	49.247	50.753	0.753±1.309	0.58
Eyeless and wing venation	65	257	130	127	50.584	49.416	0.584±2.104	0.28
Normal eye, and reduced wing	76	700	393	307	56.143	43.857	6.143±1.275	4.82
Eyeless and reduced wing	76	300	172	128	57.333	42.667	7.333±1.947	3.77
Normal eye and eyeless	266	2557	1741	816	68.088	31.912	18.088±0.667	27.12
Normal and reduced wing	110	924	517	407	55.952	44.048	5.952±1.109	5.37

TABLE 10

Showing the difference in viability between bar eye, eyeless and reduced wing and their normal allelomorphs.

CHARACTERS TESTED	2× NORMAL =N	EXPECTED NUMBER WITH MUTANT CHARACTER, THAT IS, NUMBER NORMAL	OBSERVED NUMBER WITH MUTANT CHARACTER	100×OBSERVED NUMBER ÷ N	DEVIATION FROM EXPECTED 50 PERCENT ± P. E.	DEV. ÷ P. E. DEV.	RATIO OF OBSERVED TO EXPECTED	DEV. FROM 100 PERCENT
Non-bar eye and bar eye	5878	2939	1820	30.963	19.037±0.440	43.27	61.926	38.074
Normal eye and eyeless	3482	1741	816	23.435	26.565±0.572	46.44	46.870	53.130
Normal and reduced wing	1034	517	407	39.362	10.638±1.049	10.14	78.724	21.276

normal and the deviation from the expected 50 percent of reduced wing individuals to be 5.95 ± 1.11 percent. Table 10 shows that in a theoretical population of 1034 or twice the number of normal-winged individuals only 78.7 percent of the expected reduced winged individuals were observed or that 21.3 percent failed to come through. This difference may account for the deviation observed betweeen the number of bar-eyed reduced and normal individuals.

All the tests for bar-eye were made from crosses of bar-eyed males to normal females because a female homozygous for bar is sterile. During the course of the experiment 122 bar-eyed females were tested. Of these, 121 were sterile and 1 has a record of 15 normal sons. This is either a mistake in the record which could not be detected, or this female was genetically non-bar although she had the somatic appearance of a homozygous bar individual. The cause of sterility[2] of the bar-eyed females is not known.

In table 7 are recorded all the mutants which morphologically resembled eyeless (figure 8). There were 11, all of which occurred among the treated individuals and their descendants. All of the eyeless mutants were males, 7 showed the character in both eyes, and 4 were mosaics. The 7 non-mosaic males were tested and all proved to be genetically eyeless. There was one each in the directly X-rayed, first and second generations, and 8 in the X-rayed stock. Each of these groups shows an increase over the controls in percent of eyeless mutations. Now if we exclude from each treated group and from the controls the progeny of the heterozygous eyeless females, and consider only the male progeny of the pure non-eyeless females, here, as in the case of bar, the results are not materially affected. There were 893 pure normal-eyed matings in the control group which produced 13,292 normal males. There were 2,297 males from 313 non-eyeless matings in the directly X-rayed group including 1 eyeless mutant. Therefore, the increase over the controls is 0.044 ± 0.012 percent or an increase 3.7 times its probable error. In the first generation 1 eyeless mutant occurred among 7,325 males from 591 normal females and the increase over controls is 0.014 ± 0.007 percent or twice its probable error. In the second generation, 1 eyeless mutant occurred among 4,426 from 402 pure non-eyeless females. The increase over the controls in this case is 0.023 ± 0.009 percent or an increased percentage of eyeless mutants 2.6 times its probable error. In the third generation, there were 2,837 normal males from 257 non-eyeless females. In the X-rayed stock 2 eyeless mosaic males occurred among 2,477 progeny from 173 heterozygous eyeless females. These might,

[2] Recently another new character small and its allelomorph extreme small has been produced which morphologically resembles bar in which the homozygous female is fertile.

therefore, have arisen either from binucleate eggs or as somatic mutations. The 1225 pure non-eyeless females of the X-rayed stock produced 11,453 males including 6 eyeless mutants. The increase in percentage of these eyeless mutants over the controls is 0.052 ± 0.013 percent or 4.0 times its probable error. If the treated individuals and their descendants are totaled and compared with the controls, the 9 eyeless mutants from pure non-eyeless females occurred among 28,338 males and none occurred among 13,292 males in the similar control group. The increase in percentage of eyeless mutations is 0.032 ± 0.010 percent or 3.2 times its probable error, and if we consider only those which were fertile and bred as eyeless, the increase over the controls is 0.025 ± 0.009 percent or 2.8 times its probable error. The latter figure involves the unsupported assumption that the sterile eyeless individuals from non-eyeless mothers were genetically normal.

The independent segregation of eyeless with other known characters is shown in table 9. In the first two lines of the table are the progeny of 110 F_1 females heterozygous for the factors for normal eye and eyeless and black and orange eye-color. In the case of the eyeless the eye-color can be classified by the color of the ocelli which in all of these stocks corresponds to the color of the compound eyes. The normal-eyed sons show a ratio of 50.7 percent black and 49.3 percent orange and the eyeless 51.9 percent black and 48.1 percent orange with an insignificant deviation of 1.89 ± 1.69 percent. Eye-color and the factor for eyeless segregate independently, but here as in the case of bar-eye, the eyeless sons are not represented in the same proportion as the normal eyed sons as would be the expectation. The second line of table 10 shows that if we assume the theoretical population to be twice the number of normal eyed sons only 46.87 percent of the expected eyeless individuals were observed, or that 53.13 percent fail to come to maturity.

The third and fourth lines of the table show the independent segregation of eyeless and the factor for defective wing venation. The next two lines, however, seem to show a significant deviation from the expected 50 percent in both the normal and eyeless sons for reduced and normal wing. In this group are the F_1 males from 76 females obtained from crossing normal eyed reduced males with eyeless normal winged females, and the difference between the expected and observed number of reduced individuals in both classes, here, as in the case of bar, is probably due to the failure of some of the reduced individuals to compete successfully with the normals during development.

Bar-eyed males mated to eyeless females produced normal daughters.

The progeny of 32 of these normal appearing F_1 females are shown in table 8. There were 132 normal sons, 70 eyeless, 86 bar-eye, and none which could be classed as bar-eyeless. These normal males each mated to a heterozygous bar and a homozygous eyeless female produced only normal daughters. Furthermore, if the fact that less than 50 percent of the expected eyeless individuals hatch and only 62 percent of the bar-eyed males, is taken into account, these three groups are seen to be represented in a 1 to 1 to 1 ratio as would be the expectation if bar and eyeless were independent and the fourth group bar eyeless was lethal.

There were, in addition, 58 individuals observed among the treated group and their descendants which were characterized by the absence of a part of the median vein of both primary wings (figure 10). It bore no direct relationship to the presence or absence of the factor for defect in the r_4 vein of the wing. Six of the eleven tested produced descendants with a similar defect in the median vein of the wing. The progeny like the original defective-winged individuals were highly sterile, not very vigorous, and too few in number to tell how the character was inherited. Some of the original defective-winged individuals were females so it seems very improbable that they represent recessive mutations although the F_1 females from some of the males produced a few sons with a similar defect in the median vein. The same is true of the 47 individuals with fused antennae (figure 13) and 121 vestigial wing (figure 14) individuals. Whether these are genetic changes or non-inherited somatic irregularities induced by the treatment, it is of interest to note that the directly X-rayed and each generation of their descendants showed a statistically significant excess over the controls of fused antennae, defective median vein, and vestigial winged individuals. A miscellaneous group included 23 individuals with abnormal abdomens, 23 with abnormal heads, 2 with abnormal thoraces, 3 wingless (figure 15) which may have been extreme vestigial wings, 4 with notched wings, 1 male with red eyes and 2 males with cream-colored eyes, all of which were sterile or too weak to mate.

There were also 23 sex mosaics similar in somatic appearance to the gynandromorphs reported by WHITING (1928c). Five were predominantly female, 2 predominantly male, 6 in which one-half the head and abdomen were male and the other half of the head was female, 8 in which the head was female and the abdomen male, 1 with half the head male, the rest of the head and abdomen being female and 1 with a male head and female abdomen. The individual with a half a male head and the abdomen and other half of the head female had 17 normal sons and 9 normal daughters. All of the other sex mosaics were sterile. The directly X-rayed individuals showed

an increase over the controls in percent of sex mosaics of 0.057 ± 0.021 percent or a difference 2.7 times its probable error. The descendants did not show an excess over the controls except in the third generation.

There was a general increase in effectiveness of the treatment from 1200 Roentgen units to 8000. Those treated with 1200 R units showed an increase over the controls of individuals showing somatic abnormalities of 1.54 ± 0.12 percent, those treated with 2400 R units showed an increase of 2.28 ± 0.16 percent of abnormal individuals and those treated with 8000 R units an increased percentage of 10.35 ± 0.27 percent. The percent treated ÷ percent control for the first group is $1.67 \div 0.14$ or 12.4, for the second group $2.41 \div 0.14$ or 17.9, and for the third $10.48 \div 0.14$ or 77.7 times that for the controls.

THE EFFECT OF VARIOUS DOSES OF X-RAY RADIATION ON THE FERTILITY OF THE DIRECTLY X-RAYED INDIVIDUALS AND THE FIRST, SECOND, THIRD AND LATER GENERATIONS OF THEIR DESCENDANTS

A comparison of the number of progeny per fertile mating for the control and the respective treated group is found in table 11. From 832 fertile control matings the mean number of progeny was 25.11 ± 0.61. The mean number of progeny from 198 directly X-rayed matings is 12.12 ± 0.50. The difference between the mean for the controls and the directly X-rayed is 12.99 ± 0.79 and less than half as many progeny are seen to hatch from the directly X-rayed matings as from the untreated. The first

TABLE 11

Showing the effect of X-ray radiation on number of progeny per fertile mating in directly X-rayed, 1, 2, 3 and later generations from the treatment.

GROUP	NUMBER OF FERTILE MATINGS	MEAN NUMBER OF PROGENY PER MATING ± P.E.	DIFFERENCE BETWEEN TREATED AND CONTROLS IN MEAN NUMBER PROGENY	DIFFERENCE ÷ P.E. DIFFERENCE
Controls	832	25.114 ± 0.610	..	..
Directly X-rayed	198	12.121 ± 0.498	12.993 ± 0.787	16.51
Generation 1 from X-ray	640	16.109 ± 0.404	9.005 ± 0.731	12.32
Generation 2 from X-ray	438	16.826 ± 0.434	8.288 ± 0.748	11.08
Generation 3 from X-ray	288	16.233 ± 0.521	8.881 ± 0.802	11.08
X-rayed stock	1398	14.145 ± 0.228	10.969 ± 0.651	16.85

generation of descendants from the treatment showed a difference from the controls in mean number of progeny of 9.00 ± 0.73. The mean for the second generation differs from the mean for the controls by 8.29 ± 0.75 and

that for the third generation by 8.88 ± 0.80 or essentially the same difference. The 1398 fertile females from all the later generations show a difference from the mean of 10.97 ± 0.65 which is even slightly greater than that for the three preceding generations.

All of the factors which contribute to this reduced fertility in the treated females and their descendants are not known. Some of the reduction in fertility may be due to the occurrence of lethal mutations in chromosomes which are not yet marked by any genetic character. The number of progeny for each female is based on the number which actually come to maturity, and some of the decrease in number is due to the failure of some of the progeny to come through after it has reached the pupal stage as will be discussed in the following section. No record has been kept of the number of eggs laid by these treated females so that what part of the reduction in number of hatched progeny is due to the failure of eggs which have been laid to reach the pupal stage and what part is due to a reduction in number of eggs laid is not known.

All of the treatments over 1600 Roentgen units significantly decreased the percentage of fertile matings among the directly X-rayed and their descendants. There were 95 sterile out of a total of 927 control matings or 89.8 percent were fertile. Of those treated with 1694 R units 161 out of 208 or 77.4 percent were fertile. The difference -12.35 ± 1.71 percent is 7.2 times its probable error. Of those treated with 3850 R units 167 or 58.6 percent of 285 matings were fertile. This difference is -31.16 ± 1.74 percent or 17.9 times its probable error. Of those treated with 8000 R units only 14 out of 32 or 43.8 percent were fertile. The difference or -46.0 ± 3.9 percent is 11.8 times its probable error.

THE EFFECT OF VARIOUS DOSES OF X-RAY ON THE VIABILITY OF THE TREATED INDIVIDUALS AND THEIR DESCENDANTS

The effect of the various doses of X-ray employed on the viability of the treated individuals and their descendants was measured by the proportion of the pupae which completed their metamorphosis. These data were obtained by counting the hatched individuals (checked by count of the empty pupae cases) and the pupae cases containing dried incompletely metamorphosed pupae. From the 832 fertile control matings 23,054 pupae were observed of which 20,436 or 88.6 percent were hatched. This percentage of viable pupae was significantly higher than that observed for any of the treated groups. The percentage of pupae hatched varied from 82.1 percent for those treated with 1440 R units to 65.6 percent for those treated with 2400 R units. Seventy-six and three tenths of those treated with

4000 R units hatched. This group includes the progeny of the 50 adults which were treated. Seventy-four and nine tenths of those treated with 4800 R units, 71.6 percent of those treated with 6000, and 68.7 percent of those treated with 8000 R units hatched.

A part of the effect on the viability of the directly X-rayed individuals is undoubtedly due to mechanical injury imposed on the larvae during preparation for the treatment. It is difficult to avoid such injury when it is necessary to handle these larvae during the early stages of their development. That this mechanical injury is a factor of the decreased viability of the directly X-rayed group is indicated when the results for the 96 divided matings are compared with those for the general controls. The larvae from these 96 matings were separated into a treated and control group, the latter differing from the general controls only in the fact that they had been handled exactly the same way as their treated sibs. Table 12 shows that the

TABLE 12

Showing for the divided matings the effect on viability of mechanical injury and of X-ray radiation.

GROUP	NUMBER OF FERTILE MATINGS	TOTAL PROGENY WHICH PUPATED	NUMBER HATCHED	PERCENT HATCHED	DIFFERENCE FROM CONTROL IN PERCENT HATCHED ± P.E.	DIFFERENCE ÷ P.E.	DIFFERENCE FROM CONTROL ½ MATINGS	DIFFERENCE ÷ P. E. DIFFERENCE
Controls	832	23054	20435	88.644	..	..	..	..
Control ½ divided matings	96	1351	1068	79.052	−9.592±0.611	15.70	..	..
Treated ½ divided matings	96	1462	924	63.201	−25.443±0.609	41.78	−15.851 ±1.157	13.70

control half matings had a significantly lower proportion of viable pupae than the group of general controls and that the treated half matings differed from the general controls by 25.4 percent, and from their untreated sibs by -15.85 ± 1.16 percent or a difference which was 13.7 times its probable error. A decreased viability of the descendants of treated individuals was a relatively constant feature. It was observed in the matings where all the hatched progeny appeared normal and is characteristic for the strains derived from the mutants produced by X-ray as has been observed for bar and eyeless in table 10.

DISCUSSION

The effectiveness of X-rays for modifying germ-plasm discovered by MULLER (1927) in Drosophila has been confirmed by WEINSTEIN (1928)

and others, for producing somatic mutations by PATTERSON (1927), demonstrated for radium in the same species by HANSON (1928), and independently demonstrated by STADLER (1928) for barley and maize. The WHITINGS (WHITING 1928a, 1929, WHITING and WHITING 1929, and WHITING 1930) have found X-rays effective in producing visible mutations, somatic irregularities, and reduced fertility in Habrobracon.

From the present experiment, it appears that mutations occur at a significantly higher rate among the directly X-rayed individuals than among the controls, at the orange-ivory eye-color, reduced wing, and eyeless loci, and that the bar locus shows an increase in percent of mutations in the same direction. All these mutations were observed as mosaics which is in keeping with the results of PATTERSON (1929) and GOWEN (1929) from treating larval stages of Drosophila with X-rays except that 5 of the 7 eye-color mosaics were observed in haploid males.

The descendants of the treated individuals also show an increased proportion of eye-color mosaics, bar, and eyeless mutations. In the case of the eye-color mosaics and the bar mutations the increase over the controls is statistically significant for the first, second, third and later generations. Some of the eye-color mosaics may have resulted from the fusion of two oocytes or a refusion of the polar body with the egg nucleus (WHITING and WHITING 1927). If we consider only the "orange" appearing mutants from black-ivory heterozygous females the increase in percentage over the controls is statistically significant only for the directly X-rayed and the second generation of descendants, but the first and third generations also show an increase in the same direction. If these are truly mosaic for black and ivory as has been suggested by WHITING for similar mosaics from black-ivory heterozygous females, they may have resulted from binucleate eggs. It would be of interest if it could be demonstrated that the treatment was effective in promoting the fusion of the oocytes in the descendants of the treated individuals, but, as pointed out in the text, there is at present no evidence that any of these individuals were mosaics of black and ivory, and some proved to be true orange mutations. In the case of the bar and eyeless mutations the majority proved to be true genic mutations and could not have arisen from binucleate eggs since the parents in neither case were heterozygous for these recessive factors.

Therefore, it seems probable that the appearance of orange ivory eye-color, bar and eyeless mutants among the descendants of the treated individuals is due to a process of somatic mutation stimulated by the original treatment, or the gene is a compound of elements, a part of which may be affected by the X-rays, and that these mutants, many of which are mosaic

either phenotypically or genotypically, are the result of the sorting out of mutant and non-mutant elements in the soma and germ cells of the later generations. MULLER (1928) on the other hand finds that mutations do not appear at a significantly higher rate in the descendants of the treated Drosophila than in the controls.

A significantly higher proportion of individuals showing defective and vestigial wings, and fused antennae and other somatic abnormalities which could not be tested was observed among the directly X-rayed and their descendants. These may represent either genetic changes or non-inherited somatic irregularities, but the stimulus to produce them was maintained by the descendants of the treated individuals for several successive generations as was a reduced fertility and a decreased viability.

SUMMARY

1. X-ray radiation is shown to be effective in increasing the mutation rate at the orange-ivory eye-color, reduced wing, bar and eyeless loci in the directly X-rayed individuals of the Parasitic Wasp *Habrobracon juglandis* (Ashmead).

2. The descendants of the directly X-rayed individuals for several successive generations show a statistically significant increase over the controls of individuals mosaic for eye-color.

3. The descendants of the treated individuals also show an increase in percent of bar and eyeless mutations.

4. There was a statistically significant increase over the controls in percent of individuals with fused antennae, a defect in the median vein of the wing, vestigial wing and other somatic abnormalities among the directly X-rayed and their descendants.

5. With an increase of intensity from 1200 to 8000 Roentgen units there was a progressive increase in the proportion of individuals showing somatic abnormalities, and a general reduction in fertility and decrease in viability.

6. The maximum treatment or 8000 Roentgen units increased the production of visible character changes including genic mutations and somatic abnormalities to 77.7 times that for the controls; reduced the percentage of fertile matings 46.0 percent, and decreased the proportion of pupae which hatched to 68.7 percent.

7. A significant decrease in fertility and reduction in viability was observed for the descendants of the treated individuals.

8. Two new recessive factors, bar, a factor causing a reduction in size of the compound eyes, and eyeless, causing the complete absence of the

compound eyes, were produced by X-ray and appeared to be independent of each other and of the factors for orange-ivory eye-color, defective, and reduced wing.

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STUDIES ON INHERITANCE IN PIGEONS. IX. THE CHOCOLATE-BROWN PLUMAGE COLOR[1]

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INTRODUCTION

In its intense phase, the chocolate brown type of pigmentation now known to occur in many varieties of the domestic pigeon closely resembles dilute black. In its dilute phase, it somewhat resembles yellow, though the resemblance is not so close as in the previous case. Brown is recessive to black and is also sex linked in inheritance. Except for the sex linkage of brown, the breeding relations of black, brown, and red in the pigeon may be considered analogous to those known for so many of the mammals.

Linkage in the pigeon was first reported by COLE and KELLEY (1919) for the two sex-linked factors, intensity of pigmentation, *I*, and inhibition of black, *A*. The writer has studied the linkage of black with the intensity factor, and Doctor L. E. HAWKINS (1931) has studied the linkage of black with the black-inhibiting factor. With the results of these studies now available, the three sex-linked factors noted above may be located approximately with respect to one another.

[1] Papers from the Department of Genetics, Agricultural Experiment Station, UNIVERSITY OF WISCONSIN, Madison, Wisconsin, No. 112. Published with the approval of the Director of the Station.

MATERIALS AND METHODS

The late Doctor J. METZELAAR presented the writer with the first pair of browns used in these experiments. They were brown-barred silver Pouters (Pigmy type) imported from Holland. Experiments were started at the UNIVERSITY OF WISCONSIN in 1924 and continued there for two more years. Additional experiments were begun by the writer in the Osborn Zoological Laboratory, YALE UNIVERSITY, in 1927, and conducted there until July, 1929, when they were transferred to the STORRS AGRICULTURAL EXPERIMENT STATION at Storrs, Connecticut. In the course of these experiments, browns have been obtained in the following breeds: Pouter, Homer, Maltese, Blondinette, and common pigeon; the reds and blacks were mostly Tumblers and Homers or birds of mixed breeding from other experiments.

All of the matings made at Wisconsin were kept in individual mating pens but at YALE and at Storrs a separate pen for each mating was not always provided. When this was not done, only identical matings were kept in the same pen, or in a few cases some of the P_1 matings were kept for a portion of the time with other birds where a genetic check would demonstrate any cross mating of pairs. No cases of cross mating occurred under these conditions.

OCCURRENCE AND IDENTIFICATION OF BROWN

Some of the breeds in which brown coloration occurs are: Carrier, Barb, Dragoon, Pouter, Homer, Maltese, Blondinette and other Orientals, Runt, Mondaine, Owls, Nun, and New York Flights. In most of these breeds brown has been regarded as an "off color" and is still generally so regarded.

There is good evidence for the identification of brown by some of the older writers; yet there has been much confusion of it with dun (dilute black), which it resembles quite closely in general color tone. As early as 1875 FULTON had illustrated the brown-barred silver and the dun-barred silver in a colored plate (facing p. 205) in the *Book of Pigeons*. Then, in spite of this evidence for the identification of these two types, certain erroneous statements were made which show that there was confusion in their classification.

Some years later LYELL (1887) also made important observations on brown. He states (LYELL 1887, p. 64): "There are two show shades of silvers, known as brown barred and black barred. They bear the same relationship to each other as the whole-coloured duns, found in Carriers and Barbs." The brown-barred silver represents the intense clumped phase of

brown, and the black-barred silver (or more properly the dun-barred silver) represents the dilute clumped phase of black. The "whole-colored duns" refer to true dun (dilute spread black) and to chocolate-brown dun (intense spread brown). Although LYELL made a very accurate comparison between the black and brown types, yet METZELAAR (1924) was undoubtedly the first to recognize brown clearly as a distinct type of pigmentation. He considered brown an intermediate oxidation product be-

FIGURE 1.—Four outer primaries in wing of chocolate pigeon showing the light, faded tips where the feathers have been exposed, as contrasted with the darker portions which have been protected by the overlapping feathers.

tween red and black. In a later paper (1926) he made an extended phenotypic analysis of brown by showing that it was acted upon by those factors which affect black.

In the intense spread condition, brown has a true chocolate-brown color, but in the dilute spread condition it appears very pale with somewhat of a

yellowish cast. The clumped condition is very silvery in appearance. There is considerable variability in the shade of both intense and dilute brown and some difficulty has been experienced in distinguishing readily the intensity differences. However, there has been little difficulty in distinguishing intense brown from dilute black, the older point of confusion. In order to convey a more accurate idea concerning the brown types, individual descriptions are presented in the Appendix. They are based on RIDGEWAY'S (1912) *Color standards and color nomenclature.*

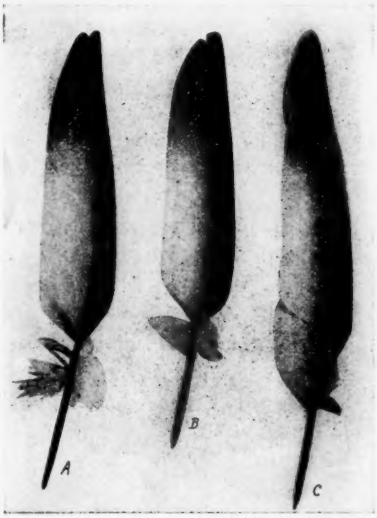

FIGURE 2.—Primary feathers arranged according to age and degree of fading. A, new feather; B, intermediate feather; C, old feather.

LYELL (1887) made the important observation that brown "often fades with the advancing year," and METZLAAR has also emphasized this characteristic of brown. Fading is very pronounced at the distal end of primaries where they are continually exposed to strong light, the faded area contrasting noticeably with the portion which has been covered by adjacent feathers (figures 1 and 2). The wing coverts also fade, but more uniformly, and for this reason the fading may be overlooked until the period of moulting. At that time such a mixture of old and new feathers gives the bird a peculiar mottled appearance. The fading of black and red may also

be observed, but it is ordinarily only slight in degree compared with that for browns.

THE JUVENILE EYE COLOR AND ITS RELATION TO PLUMAGE COLOR

The dilute browns in the young nestling stage have eyes with only a very small amount of pigment, resembling the albino eyes of other animals. Intense browns and dilute blacks have eyes which may approach this condition, but it is very soon lost. This eye character has been of considerable value in the identification of the color type to which certain birds belong. In some dilute browns the eyes remain almost unchanged from the early squab stage, but in others the eyes gradually acquire considerable pigment and at maturity can not be distinguished with certainty from those belonging to other color types.

CHRISTIE and WRIEDT (1923) have also reported the juvenile albinistic eye associated with yellow. They state (1923, p. 295): "Albino-Augen mit ganz unpigmentierter Iris und Retina kommen bei Tauben gewiss nicht vor. Wir haben eine Anzahl Individuen gehabt, alle gelb, die im Nestkleid diese Augenfarbe gehabt haben, aber nach der Mauser ist die Retina immer pigmentiert worden, so dass die Pupillen sich schwarz wie bei den anderen Typen der Augenfarbe gezeigt haben. Die zweifelfreien Fälle dieser Art haben alle beinweisse Iris im erwachsenen Alter gezeigt."

In canaries, DURHAM and MARRYAT (1908) observed a similar condition associated with cinnamon (chocolate brown), and concerning this character they state (1908, p. 57): "In ordinary canaries the eyes on hatching look black, but in cinnamons they look pink. The eyes become dark in appearance as the birds grow older, so that in the adult cinnamon it is extremely difficult if not impossible to distinguish the color of its eye from that of an ordinary canary by simple inspection. Microscopical examination, however, shows that the pigment of the cinnamon eye is different from that of the normal eye, being chocolate only, and not black."

Preliminary histological studies on pigeon eyes have shown that the "albino" eye of the dilute chocolate is due to the very limited deposition of pigment in the retina and choroid coat. Thus far we have not been able to detect differences in the kind of eye pigments in blacks and browns.

BREEDING RELATIONS OF BLACK, BROWN, AND RED

Survey of the literature

Black-red

COLE (1911, 1914) was the first to study adequately the breeding relations of black and red. He found black dominant to the ordinary type of

red, and used the factors: *B* for black, *b* for red. In the present paper COLE's factorial scheme will be modified slightly.

Black-brown

The two Norwegian workers, CHRISTIE and WRIEDT (1927), first demonstrated that brown is recessive and sex linked in relation to black. This was soon confirmed by STEELE (1928). It is interesting to note, however, that there is good evidence for this relationship of brown in DARWIN'S discussion of the breeding results with silver Dragoons, in which he states (1871, p. 446): "When TEGETMEIER at last got a silver male and matched him with one of the silver females, he expected to get a breed with both sexes thus colored; he was however disappointed, for the young male reverted to the color of his grandfather, the young female alone being silver." It is now plainly evident that TEGETMEIER crossed a brown-barred silver male with a dun-barred silver female, and that the blue male resulted according to present-day expectation (see matings W-2071 and Y-50, table 1). A similar erroneous conclusion is drawn by LUMLEY in the 1895 edition of FULTON. He states concerning the breeding of brown-barred silvers (1895, p. 275): "Now and then they may breed a fair Blue, reverting to the color whence they sprang . . . ."

In the canary, DURHAM and MARRYAT (1908) have shown that brown is also recessive and sex linked in inheritance. A more complete report was later made by DURHAM (1926), and in this paper the aberrant cases were considered in more detail.[2]

Brown-red

METZELAAR (1928) and STEELE (1928) have studied brown in relation to red (recessive red of COLE), and have found that brown×red matings may throw blacks and browns, as well as recessive reds and dominant reds, depending upon the constitution of the P_1 birds. Both workers agree that an extension factor is involved in the development of black or brown, and that red develops when this extension factor is absent.

Experimental results

Black-brown

Data from reciprocal matings of black × brown are presented in table 1, and an inspection of the actual results will show that they are in close agreement with the expected. Three matings of black ♂ × brown ♀ gave 14 blacks, in the ratio of 9 males to 5 females, whereas the expected ratio

[2] See also DUNCKER (1928).

is 7:7. The four reciprocal matings, brown ♂ × black ♀, gave 15 black males:17 brown females, compared with an expected ratio of 16:16.

TABLE 1

Reciprocal matings of black×brown.

	TYPE OF MATING	MATING NUMBER*	PARENTS		OFFSPRING				
					Black		Brown		Total
			♂	♀	♂	♀	♂	♀	
A	Black ♂ *BB*	W2193	2130A	2136A	1	1	0	0	2
	——	Y44	13A	14A	5	3	0	0	8
	Brown ♀ *b*—	Y98	18A	22A	3	1	0	0	4
	Total				9	5	0	0	14
	Expected				7	7	0	0	..
B	Brown ♂ *bb*	W2071	2039A	1942C	3	0	0	1	4
	——	Y50	25A	5A	8	0	0	6	14
	Black ♀ *B*—	Y118	21A	36A	2	0	0	6	8
		Y50 or	Y118†		2	0	0	2	4
		S148	122F	5A	0	0	0	2	2
	Total				15	0	0	17	32
	Expected				16	0	0	16	..

* The letter preceding the mating number refers to the place where the mating was made: W—Wisconsin; Y—Yale; S—Storrs. This applies to all of the tables.

† Complete identification lost due to late banding. The two matings were kept in the same pen for a portion of the time.

Segregation for brown in the heterozygous F_1 black males has been tested by mating such males with either black or brown females. The data are presented in table 2 and are grouped according to the type of mating. Part A includes the matings of F_1 males × black females, and Part B includes matings of F_1 males with brown females. It is very evident that the results in Part A represent a poor fit when compared with the theoretical, but the numbers are small and no great weight can be attached to this deviation. The actual results were, 2 black ♂♂:0 black ♀:5 brown ♀♀; the expected ratio when sex is considered is 3.5:1.75:1.75, and when it is disregarded, 5.25 blacks:1.75 browns. The 15 matings of F_1 ♂×brown ♀ resulted in 62 blacks:60 browns, whereas the expected ratio is 61:61. If sex is considered and we use those birds whose sex record is complete, the results are as follows: 26 black ♂♂:32 black ♀♀:33 brown ♂♂:25 brown ♀♀. The expected ratio is 29 in each class.

The data presented above fully confirm the conclusions of CHRISTIE and WRIEDT that brown is recessive and sex linked in relation to black.

Brown-red

Reciprocal matings of brown×recessive red are listed in table 3. When the male parent is red and the female brown, blacks occur in both sexes in

TABLE 2

Matings of F_1 black males×black and brown females.

	TYPE OF MATING	MATING NUMBER	PARENTS ♂	PARENTS ♀	OFFSPRING Black ♂	Black ♀	Black ?*	Brown ♂	Brown ♀	Brown ?*	Total
A	Black ♂ *Bb*	Y131	50J	8A	1	0	..	0	2	..	3
	Black ♀ *B*—	S152	47B2	36A	1	0	..	0	3	..	4
	Total				2			5			7
	Expected				5.25			1.75			..
B	Black ♂ *Bb*	Y-S121	50G	42A	3	0	..	1	6	1	11
		Y122	50F	22A	3	2	..	2	0	..	7
	Brown ♀ *b*—	Y-S123	47E	50B	1	1	..	4	3	..	9
		Y124	50E	50A	1	3	..	1	0	..	5
		Y-S132	47F	50K	1	3	..	1	1	..	6
		Y-S137	50N	126J	1	4	1	3	3	..	12
		Y-S139	50U	121A	2	2	1	3	3	..	11
		Y-S141	50S	126K	3	4	..	3	3	..	13
		Y-S142	50V	121F	4	1	1	2	2	..	10
		Y-S144	50F	126F	3	1	..	2	2	1	9
		Y-S145	50J	131C	2	2	..	5	0	..	9
		Y-S146	50E	126H	1	3	1	3	2	..	10
		S149	37S	22A	0	2	..	1	0	..	3
		S151	47P	50T	1	4	..	0	0	..	5
		S154	47Y	50H	0	0	..	2	0	..	2
	Total				26	32	4	33	25	2	122
					62			60			
	Expected				61			61			

* Sex record not obtained.

the F_1. In the reciprocal matings, brown male×red female, the results are similar to those from matings of brown male×black female, in which the males are black and the females brown. It will be noted that the results in either type of mating may be modified if the *A* factor is carried by the reces-

sive red parent. If the *A* factor is involved in the first type of mating, the dominant reds may occur in both sexes in the F_1, but if in the second type, then dominant reds will occur only in the male class and the females will be brown.

TABLE 3

Reciprocal matings of brown×recessive red.

	TYPE OF MATING	MATING NUMBER*	PARENTS ♂	PARENTS ♀	OFFSPRING Dominant Red ♂	Dominant Red ♀	Black ♂	Black ♀	Brown ♂	Brown ♀	Recessive Red ♂	Recessive Red ♀	Total
A	Recessive Red ♂ *(BBA)Aee* / Brown ♀ *ba−E(E)*	W2190	2095A	2124A	1	2†	0	0	0	0	0	0	3
A	*(BBA)Aee* / *ba−EE*	W2194	2187A	2036A	1	0	0	0	0	0	2	0	3
A	*(BBAA)ee* / *ba−E(E)*	W2197	2095A	2125A	1	2	0	0	0	0	0	0	3
A	*BBaaee* / *ba−EE*	Y47	28A	2A	0	0	6	9	0	0	0	0	15
A	*BBaaee* / *ba−EE*	Y97	26A	1A	0	0	3	6	0	0	0	0	9
A	Total						9	15					
A	Expected						12	12					
B	Brown ♂ *ba ba EE* / Recessive Red ♀ *(B)A−ee*	W2196	2039A	1888G2	1	..	..	..	..	3	..	..	4
B	*babaE(E)* / *(Ba)−ee*	Y42	21A	16A	0	..	0	..	..	2	..	..	2
B	Total				1	..	0	..	..	5	..	..	6
B	Expected					3		..	..	3	..	..	..

* Parenthesis is used to indicate the portion of the formula not fully established by observation or breeding behavior.

† Sex record incomplete.

The two recessive red ♂×brown ♀ matings in which the *A* factor was not involved (Y47 and Y97) produced 9 black ♂♂:15 black ♀♀, compared with an expected ratio of 12:12. There were also three matings in which the *A* factor was involved (W2190, W2194, and W2197) and they

gave 7 dominant reds:2 recessive reds. Since these birds have not been tested as to their genetic constitution, we must omit them from any further consideration at this time.

Data from the reciprocal matings, brown ♂ × recessive red ♀, are very limited but are in agreement with the expected results. The first mating, W2196, involved the *A* factor and resulted in 1 dominant red ♂:3 brown ♀ ♀; the expected ratio is 2:2. The other mating, Y42, gave only the 2 brown females. Unfortunately no black males were reared from this type of mating.

Factorial analysis

The breeding data presented for black, brown, and red show that their genetic relationships may be interpreted upon a two factor hypothesis. In a previous paper the writer has presented such a hypothesis, which is similar to the one by METZELAAR (1928) except that the usage of terms is made to conform with that commonly employed for mammals.

The factors are:

B—factor for black
b—factor for brown
} sex linked

E—factor for extension of black or brown
e—factor for non-extension of black or brown

Phenotypes: *BE*—black; *bE*—brown; *Be*—red; *be*—red.

In the reds of good color it is not possible to distinguish the two genotypic types noted above, but in some birds of defective coloration, in which the rump and tail appear slaty, there may be enough black or brown present to reveal the presence of *B* or *b*.

LINKAGE OF BROWN AND INTENSITY OF PIGMENTATION

The individuals used to test the linkage between brown and intensity of pigmentation were the double heterozygous males which appeared in matings W2071, Y50, and Y47. The first two matings, W2071 and Y50, were of the following type: intense brown *bI/bI* ♂ × dilute black *Bi* ♀; and, in the last mating, Y47, a dilute red (*Bi/Bi*) (*e/e*) ♂ was mated with an intense brown *bIE/E* ♀. All of these matings produced intense black *Bi/bI* males. Until dilute brown *bi* females were available the males mentioned above were crossed with other females such as, intense black *BI*, dilute black *Bi*, intense brown *bI*, or dilute red *Bi*(*e/e*). From such matings only the female offspring may be used for calculating the linkage value because the crossovers form a distinctive class only in this sex. The double recessive females of constitution *bi* which appeared as crossovers in the mat-

ings considered above were used as soon as they matured, and from such matings all of the offspring may be used for the linkage data.

For a portion of the time that the experiments were in progress at YALE, and later at Storrs, several matings of the first type were kept in one large pen. During this period some birds were not banded before they left the nest and their complete identification as to mating could not be determined. Such birds were given a group number (126) and a letter according to the order of occurrence. Since all of these birds come from the same type of mating there seems to be no reason to exclude them from the results. All of the matings of the second type were kept in individual mating pens and there can be no question about their parentage.

Experimental results

Matings of *Bi/bI* males × females of other than the *bi* type are listed in Part A of table 4. From these matings only the female offspring are recorded. The non-crossover classes are composed of dilute blacks, and intense browns, whereas the crossover classes are composed of intense blacks and dilute browns. There were 17 crossovers:34 non-crossovers, which is the equivalent of 33.3 percent of crossing over.

The matings of the second type, *Bi/bI* ♂ × *bi* ♀, are listed under Part B of table 4, and in this group the crossovers form distinctive classes in both sexes. There were 7 matings and they produced 29 crossovers:46 non-crossovers, which is the equivalent of 38.7 percent crossing over. It will be noted that there is some difference between the crossover values from the two sets of data, but the differences are probably due only to chance. Data from the two groups may be combined since the expected results in the female classes of Group A are the same as the expected results for the male and female classes of Group B. The combined data give 46 crossovers:80 non-crossovers, which is the equivalent of 36.5 percent of crossing over. From these results we may infer that there is only a loose linkage between the factors *B* and *I*. The difference between this value for *I-B* and COLE and KELLEY's determination for *I-A* is only 3.2 and would indicate that *B* and *A* are very close together. HAWKINS (1931) has, as a matter of fact, not been able to demonstrate any crossing over between *B* and *A*.

SUMMARY AND CONCLUSIONS

The chocolate brown plumage color of the domestic pigeon represents a mutation from black, and is very widely distributed throughout the various breeds of pigeons. In general color tone it resembles brown of other birds

and mammals. It is recessive and sex linked in relation to black. In the canary, brown is also recessive and sex linked, but in mammals no relationship to sex has been reported. The very wide occurrence of brown coloration throughout the animal kingdom may be considered as evidence for

TABLE 4

Matings showing linkage of B and I.

	MATING NUMBER	PARENTS ♂ Number	♂ Formula	♀ Number	♀ Formula	OFFSPRING† non-Crossover *Bi*	non-Crossover *bI*	Crossover *BI*	Crossover *bi*
	W2180	2071J	*Bia·bIaEE*	2037A	*BiA−ee*	0	1	0	0
	Y-S121	50G	*Bi·bI*	42A	*bI−*	0	3	0	3‡
	Y122	50F	*Bi·bI*	22A	*bI−*	2	0	0	0
	Y-S123	47E	*Bi·bI*	50B	*bI−*	1	2	0	1
	Y124	50E	*Bi·bI*	50A	*bI−*	3	0	0	0
A	Y-S126*					7	6	1	6
	Y131	50J	*Bi·bI*	8A	*Bi−*	0	1	0	1
	Y-S132	47F	*Bi·bIEe*	50K	*bI−Ee*	2	1	1	0
	S149	47S	*Bi·bI*	22A	*bI−*	1	0	1	0
	S151	47P	*Bi·bI*	50T	*bI−*	3	0	1	0
	S152	47B2	*Bi·bI*	36A	*BI−*	0	1	0	2
	Total					19	15	4	13
	Y-S137	50N	*Bi·bI*	126J	*bi−*	2	3	4	3
	Y-S139	50U	*Bi·bI*	121A	*bi−*	2	4	3	2
	Y-S141	50S	*Bi·bI*	126K	*bi−*	5	5	2	1
B	Y-S142	50V	*Bi·bI*	121F	*bi−*	5	1	1	3
	Y-S144	50F	*Bi·bI*	126F	*bi−*	1	3	3	2
	Y-S145	50J	*Bi·bI*	131C	*bi−*	2	6	2	0
	Y-S146	50E	*Bi·bI*	126H	*bi−*	3	4	2	1
	Total					20	26	17	12

Summary: 80 non-crossovers, 46 crossovers.

Percent crossing over, 36.5.

* Birds reared in large pen containing several mated pairs (Group A), and identification as to particular mating lost due to late banding.

† "Offspring" in Group A includes only females; in Group B both sexes are included.

‡Exclusive of a bird recorded as Dilute Brown Check, but whose sex record is incomplete.

the mutability of the black factor. Brown and black bear the same relationship to red. They are expressed only when a dominant extension factor (*E*) is present. When this extension factor is absent the bird is red.

Strong light causes brown to fade in a very characteristic manner, and this is usually most marked at the distal end of the primary feathers. Though fading is not restricted to brown, it is more conspicuous in browns than in reds or blacks.

The eyes in young dilute brown squabs appear like albino eyes but gradually become darker as the birds approach maturity. The juvenile albinistic eye has been reported for yellow pigeons by CHRISTIE and WRIEDT, and also for the cinnamon-colored canary by DURHAM and MARRYAT. The last named authors observed further that the normal eye possessed black pigment and that the pink eye had brown pigment. In preliminary histological studies on the pigeon eye we have not observed differences in the kind of pigment, but have found pronounced differences in the amount of pigment present in the retina and choroid of the intense blacks and dilute browns. In this regard our observations differ from those of DURHAM and MARRYAT on the "pink-eye" of the cinnamon canary.

Brown shows linkage with the factors for intensity (*I*) and inhibition of black (*A*). With the first factor the linkage is very loose (36.5 percent), but with the second HAWKINS has found perfect linkage. Previous to these studies COLE and KELLEY had determined the linkage of intensity and inhibition of black (39.7 percent). Upon the basis of these results the three sex-linked factors, *B*, *I*, and *A*, may be approximately located.

Individual descriptions are presented in the Appendix. They are based on Ridgeway's *Color standards and color nomenclature.*

The writer desires to express his gratitude to Professor L. J. COLE for his encouragement and helpful suggestions given during the progress of this study; to Doctor ROSS G. HARRISON of YALE UNIVERSITY, and to Doctor WALTER LANDAUER of the STORRS AGRICULTURAL EXPERIMENT STATION for the generous provisions they have made for its continuance in their respective departments. It is also very fitting that the writer should pay his respects to the memory of the late Doctor JAN METZELAAR of the MICHIGAN STATE DEPARTMENT OF CONSERVATION for generosity in providing some of the original stock and for his continued interest in this problem.

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APPENDIX. COLOR DESCRIPTIONS OF CHOCOLATE BROWN TYPES

The following color descriptions of brown birds were made according to RIDGEWAY'S (1912) *Color standards and color nomenclature.*

Intense types[3]

2124 A—Brown Maltese

General color corresponds to Bister (Ridgeway's Plate 29). The faded portion of an old tail feather corresponds to Prouts Brown (15).

2136 A—Brown checker Maltese

Spread areas of wing coverts correspond to Mars Brown (15). The clumped or checked areas correspond to Pale Drab Yellow (46). The terminal bar of tail corresponds to Clove Brown (14). The middle region though difficult to match seems closer to Ecru Drab (46) than to any other color.

2039 A—Brown silver Pouter

The general color of the wing coverts is silvery with a slight creamy yellow cast, and there is a sooty effect upon many of the coverts. The lesser wing coverts correspond to Pallid Purplish Gray (53). The interscapular coverts correspond to Cartridge Buff (30) or to Tilluel-Buff (40). The wing bars are close to Clove Brown (40) or to Bister (29). The unfaded tips of new primaries correspond to Wood Brown (40); in the middle region the amount of brown is greatly reduced. New tail

[3] Miss AGNES ZEIMET, Technician in the Department of Genetics, UNIVERSITY OF WISCONSIN, assisted in the color descriptions of this group. They were made October 20, 1925, when the birds had nearly completed the moult.

feathers: middle region, Pale Mouse Gray (40); terminal bar, Bister (29). Old tail feathers: middle region, Pale Mouse Gray; terminal bar, Raw Umber (3).

2071 D—Brown Silver

The general color essentially the same as for 2039 A. Old primaries show pronounced fading at tips, and these areas correspond to Cartridge Buff (30).

Dilute types[4]

152 D—Dilute brown checker

(Seven weeks of age, and reared in room away from strong light.) The spread areas of the wing coverts are closer to Drab (46) than to any other color; the clumped or checked areas correspond to Carbon Gray (53) or to Pallid Mouse Gray (51) though somewhat lighter than the last named color. Wing bars somewhat darker than Drab (46). Primaries Pale Drab Gray (46). Proximal portion of tail feathers Drab Gray; terminal bar slightly darker than Drab.

126 H—Dilute brown checker

General color Drab (46), but mixture of old and a few new feathers gives a variegated effect.

148 A—Dilute brown silver

General color of wing coverts light creamy with some yellowish cast; wing bars and tail bar very pale brown. The wing coverts correspond to Tilluel-Buff (40); the upper wing bar to Drab (46); the lower wing bar is lighter and more like Light Drab (46). New primaries correspond to Pale Drab (46); old primaries are much lighter. Proximal portion of tail feathers, Pale Drab Gray (46); terminal bar, Drab (46).

[4] Descriptions made July 24, 1930. Adult birds were just beginning to moult.

STUDIES ON INHERITANCE IN PIGEONS. X. RELATION OF CHOCOLATE TO BLACK AND DOMINANT RED[1]

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INTRODUCTION

Numerous color variations in the domestic pigeon have been studied by the geneticist. Until recently, investigations of the subject suggested that these several color effects were due to different combinations and arrangement of but two basic pigments. These two kinds of pigments, black and red, in varying degrees of intensity and under various influences of distribution, have been regarded as entirely responsible for the appearance of all colored breeds of pigeons. White has been recognized as a factor in color arrangements also, but white, being an absence of pigment, has in no way changed the idea that only two basic pigments exist.

More recently (METZELAAR 1926), however, a third basic pigment, chocolate, was recognized. Subsequent study has conclusively shown that chocolate cannot be included with either black or red, but must be consid-

[1] Papers from the Department of Genetics, Agricultural Experiment Station, UNIVERSITY OF WISCONSIN, Madison, Wisconsin, No. 113. Published with the approval of the Director of the Station.

ered in a separate category. The recognition of this third kind of pigment has done much to correct certain erroneous ideas of color inheritance. The discovery of chocolate in the pigeon is of further interest to the evolutionist. Three pigments, black chocolate and red, with various modifications, are thought to produce all the different colors found in the hair of mammals; the same three pigments have been demonstrated in the plumage of birds.

Two kinds of red, genetically different, have been reported (COLE 1914, COLE and KELLEY 1919) in the pigeon. The first observed was shown to be inherited as a single factor recessive to black, and autosomal. It is called "recessive red." The other, "dominant red," was reported as dominant (or epistatic) to black, and sex linked. A genetic factor for intensity of color (COLE 1912) also has been shown to be inherited in sex-linked fashion. Soon after the recognition of chocolate in the pigeon this color was demonstrated (CHRISTIE and WRIEDT 1927) to be sex linked and recessive to black. The present study was undertaken to determine linkages of these sex-linked genes. In the course of the work some very interesting relations of chocolate to dominant red and black have been brought to light.

This project was begun at the UNIVERSITY OF WISCONSIN, and later transferred to Oklahoma. Helpful suggestions have been made by Doctor L. J. COLE, who has supervised the experiment, and his assistance in the matter of facilities and stock is deeply appreciated. Professor W. L. BLIZZARD and other authorities of the OKLAHOMA AGRICULTURAL AND MECHANICAL COLLEGE have provided facilities for continuance of the work.

CHARACTERS

Black

JONES (1922) described six different color patterns in the pigeon based on differences in the distribution of black pigment in the feathers. She reported these as constituting an epistatic series, which she designated in the following order, beginning with the highest member in point of dominance: self black, black with blue tail, black check, sooty, blue barred and blue barless. BOL (1926) recognizes the same grades of modification, but believes they form a multiple allelomorphic rather than an epistatic series.

This series is distinguished by the relative amounts of black and "blue" in the plumage. In the black areas the black pigment is spread evenly throughout the respective cells of the barbules of the feather, resulting in an even black optical effect. The so-called "blue" is really a neutral gray due to the clumping of the black pigment granules in the barbule cells so that they have a beaded appearance under the microscope. The gross optical

effect is the gray commonly designated as "blue." The series really depends, therefore, on the extent to which "spread" pigment has been replaced by "clumped."

Dominant red and gray

COLE in 1909 reported red in the pigeon as a simple Mendelian recessive to black. In a later paper (1914) he discussed this type of red more fully. It was described as essentially uniform in its distribution over the entire body, wings and tail. Another kind of red was later described by COLE and KELLEY (1919); this was shown to be dominant to black and sex linked. The symbol *A* was assigned to it.

These authors interpret the action of *A* as a modification of black to red and gray, or possibly gray without red, depending on the presence of modifying factors. More will be said presently about gray. They further state:

"A characteristic of all dominant red birds .... is a peculiar lightening of the tail that we have often in our records referred to as a 'washed out appearance.' The tail is in all cases noticeably different from the body, even in birds which without *A* would have their pigmented areas uniformly colored."

COLE and KELLEY called attention to the homology between the dominant red and black series, suggesting that in general the same factors control distribution of both black and dominant red pigment. BOL (1926) has further described and classified dominant red birds into types homologous to classes of the black series.

COLE and KELLEY (1919) regarded dominant gray as due to the same *A* factor which produces dominant red. They say regarding it:

"Whether an *A* bird shows red or gray probably depends on some unidentified factor or factors which modify the action of *A*; although the possibility that the gray-producing *A* is a third allelomorph in the set must be considered."

Some of the dominant grays have a small sprinkling of red ("mealiness") in the region of the wing bars and on the head and neck, or in some cases there may be noticeable "flecking" of black or chocolate over various parts of the body.

The inheritance of gray has not yet been adequately analyzed, but certain observations indicate that it is not an allelomorph of black and dominant red. Gray females mated to black and to blue males have produced only black daughters and gray and dominant red sons. This confirms the sex linkage of gray, but the female pigeon is simplex for sex-linked genes, and the fact that both gray and dominant red sons were produced from

gray mothers proves that gray, dominant red, and black are not in the same allelomorphic series. While gray and dominant red often intergrade, the above statement is based on unmistakeable types of progeny.

Chocolate

The first positive mention of chocolate pigment in the plumage of the pigeon was made only a few years ago (METZELAAR 1926), although this color is widely distributed among domestic races. METZELAAR pointed out a close analogy between corresponding types of the black and chocolate series. A year later chocolate pigmentation in the pigeon was shown by CHRISTIE and WRIEDT (1927) to behave as a Mendelian recessive to black, and to be sex linked. Homozygous black males mated with chocolate females produced only black offspring. Chocolate males, when mated to black females, produced all black male offspring, and all chocolate female offspring. Black males, heterozygous for chocolate, mated with chocolate females produced offspring of both sexes, half of which were black and the other half chocolate. Later work of METZELAAR (1928), STEELE (1928, 1931), and this experiment confirms the report of CHRISTIE and WRIEDT. WRIEDT and CHRISTIE (1925) mention a form of "braun," but it evidently differs from the chocolate described by them in 1927. They discuss matings of "schokolade×homozygotisch braunem" in the latter paper showing that they consider the two to be genetically different. They postulate a dominant autosomal factor *B* for "braun" (1925), but consider it to be hypostatic to *R*, their factor for black. Careful analysis of their tables reveals discrepancies which may have been caused by the presence of chocolate birds in their stock. Their data could be analysed more fully if they had designated the sexes in their matings. Table 3, c, in their paper shows at least one mistake. The mating is labelled "Braun×recessivem Rot" but the formulae of the birds mated are *rrBb*×*rrBb*. According to their previous statements both these birds would be "braun." Furthermore they list two black offspring among the progeny of this mating. Black, according to them, is produced by *R;* consequently no black offspring should have been produced by parents both of which were *rr*.

COLE and KELLEY (1919, p. 186 footnote) suggested that black in the pigeon is homologous to black in rodents, in that the black pigmentation is due to a factor for extension of this pigment. STEELE (1928, 1931) adopts this suggestion and uses a set of genetic symbols for basic colors in the pigeon similar to those in rodents. He employs the symbol *E* for the extension of black, chocolate, and dominant red pigment; recessive red is represented by *e; B* indicates black; *b*, chocolate. Dominant red retains the

symbol *A*; its absence (black or chocolate) is represented by *a*. *B* and *A* are sex linked. A black bird, then, would be *EBa*, a chocolate *Eba*, and a dominant red *EB*(or *b*)*A*. All *ee* birds would be recessive red regardless of *B* or *A*.

A special effort to secure crossovers between *B* and *A* has been made in the present work but none have appeared. This apparent complete linkage of *B* and *A*, together with other evidence which will be presented shortly, strongly suggests that dominant red, black, and chocolate constitute a series of multiple allelomorphs. Consequently a change will be made in the above symbols. Black pigment is found in the wild Rock pigeon, which is generally accepted as the wild type of *Columba livia*, and *B* will be retained to represent the gene which produces black. Chocolate is recessive to black and the gene for chocolate will accordingly be indicated by *b*. But dominant red is dominant to both black and chocolate. Since *A* has been used heretofore to designate dominant red the symbol B^A instead of *A* is suggested. Taking the *E* factor into consideration, a black bird would be *EB*, a chocolate *Eb*, and a dominant red EB^A. All *ee* birds would be recessive red as STEELE suggested.

At least five color patterns of chocolate, based on distribution of pigment as in the black-blue series, have been observed in the course of this work, and it seems probable that all six patterns exist. This classification has not been definitely established genetically, but it seems very probable that chocolate pigment is distributed over the bird and the individual feathers in a manner similar or identical to the distribution of black and dominant red. The same set of genetic factors undoubtedly controls the distribution of all three kinds of pigment.

All the classes within a series may be considered collectively in so far as this work is concerned. The study is of the relations of the different kinds of pigment, black, red, and chocolate with one another, without regard to the mode or degree of distribution of the pigment over the body of the bird. Hence in further reference to colors, unless otherwise indicated, it will be understood that black includes all six classes possessing black pigment and similarly for dominant red and chocolate.

Intensity

COLE (1912) described the action of an intensity factor in the pigeon; COLE and KELLEY later (1919) discussed its inheritance more fully, and reported linkage between it and dominant red. Intense pigmentation includes black and red, while dun and yellow are corresponding dilute colors. METZELAAR (1926, 1928) demonstrated a similar situation in chocolate, in which he designated the intense form as chocolate and the dilute form

drab. The same factor difference (*Ii*) is responsible for the intensity difference in all three kinds of pigment.

The difference between intense and dilute pigmentation in the pigeon is one of amount rather than kind of pigment (LLOYD-JONES 1915). In general it may be said that the pigment granules in the intensely colored bird are much more numerous and packed closer together than in the dilute feather. This causes the former to absorb more light, and consequently they are much darker in color than the latter.

The intensity factor, *I*, is sex linked in the pigeon, and intense pigmentation is dominant to dilute (COLE 1912). Intense females, mated to dilute males, produce all intense sons and all dilute daughters, and homozygous intense males produce all intense offspring regardless of whether the female parent is intense. The studies of COLE and KELLEY (1919) and CHRISTIE and WRIEDT (1923) show the genes for dominant red and intensity to be widely separated on the sex chromosome; COLE and KELLEY reported 39.72 percent crossing over between the two. No exceptions in the relations between these two genes have occurred in the present work, but the indication is that they are even more loosely linked than previously reported.

RESULTS AND DISCUSSION

The dominant red and black birds used in this project were principally of Homer and Tumbler breeding. Chocolate was introduced from Pouter stock. Only a few birds were of pure breeding but pedigree records of all of them have been kept. The stock has been used in genetic experiments at Wisconsin for many years, and the ancestry of the birds used is known. All matings were carefully controlled, and daily records have been made throughout the experiment.

Breeding

Dominant red,[2] black, and chocolate

Matings of black with chocolate produced results in agreement with the findings of other workers (CHRISTIE and WRIEDT 1927, METZELAAR 1926, 1928, STEELE 1926, 1928). Homozygous black males mated with chocolate females ($BB \times b-$, table 1, 7) produced only black offspring, both males and females, which confirms the complete dominance of black over chocolate. The reciprocal cross, chocolate male $\times$ black female ($bb \times B-$, table 1, 5) gave black male and chocolate female offspring, and shows the sex linkage of black and chocolate.

[2] As previously noted (p. 549) "dominant red" includes all modifications of dominant red and gray phenotypes.

TABLE 1

Showing dominance of dominant red over black and chocolate, of black over chocolate, and sex linkage of dominant red, black and chocolate.

TYPE OF MATING			DOMINANT RED			BLACK			CHOCOLATE			TOTAL COLOR		
Phenotype	Genotype		♂	♀	Sex?	♂	♀	Sex?	♂	♀	Sex?	D.R.	Black	Chocolate
Chocolate ♂	*bb*	Observed	32	..	5	..	..	..	..	40	2	37	..	42
1 ×	×													
Dominant red ♀	B^A-	*Expected*	*36*	..	*3.5*	..	..	..	..	*36*	*3.5*	*39.5*	..	*39.5*
Dominant red ♂	B^Ab	Observed	46	54	5	..	..	..	47	45	5	105	..	97
2 ×	×													
Chocolate ♀	*b*−	*Expected*	*48*	*48*	*5*	..	..	..	*48*	*48*	*5*	*101*	..	*101*
Dominant red ♂	B^AB^A	Observed	2	4	3	..	..	..	..	..	..	9	..	..
3 ×	×													
Chocolate ♀	*b*−	*Expected*	*3*	*3*	*3*	..	..	..	..	..	..	*9*	..	..
Dominant red ♂	B^AB	Observed	1	2	7	10	11	5	..	..	..	10	26	..
4 ×	×													
Chocolate ♀	*b*−	*Expected*	*6*	*6*	*6*	*6*	*6*	*6*	..	..	..	*18*	*18*	..
Chocolate ♂	*bb*	Observed	..	..	..	8	..	9	..	11	3	..	17	14
5 ×	×													
Black ♀	*B*−	*Expected*	..	..	..	*9.5*	..	*6*	..	*9.5*	*6*	..	*15.5*	*15 5*
Black ♂	*Bb*	Observed	..	..	..	33	20	15	27	30	9	..	68	66
6 ×	×													
Chocolate ♀	*b*−	*Expected*	..	..	..	*27.5*	*27.5*	*12*	*27.5*	*27.5*	*12*	..	*67*	*67*
Black ♂	*BB*	Observed	..	..	..	5	2	1	..	..	..	..	8	..
7 ×	×													
Chocolate ♀	*b*−	*Expected*	..	..	..	*3.5*	*3.5*	*1*	..	..	..	..	*8*	..
Black ♂	*Bb*	Observed	..	..	..	3	1	1	..	1	..	..	5	1
8 ×	×													
Black ♀	*B*−	*Expected*	..	..	..	*2.5*	*1.25*	*0.75*	..	*1.25*	*.25*	..	*4.5*	*1.5*

Black males known to be heterozygous because one of the parents was chocolate mated with chocolate females and produced black and chocolate offspring of both sexes (table 1, 6). The numbers of black and chocolate progeny are very near equality although they are not very evenly distributed according to sex. A mating of a heterozygous black male with a black female (table 1, 8) produced black males, a black female, and a chocolate female. The number of progeny here is small but the types secured are as expected. These results further show that chocolate is inherited as a single Mendelian factor, sex linked, and recessive to black.

The dominant red birds used as parent stock in this work were descended from strains which were entirely free from chocolate. These birds were principally of Homer and Tumbler breeding. They were mated with chocolate birds to produce F_1 males heterozygous for dominant red and for chocolate. Chocolate males (*bb*) mated with dominant red females (B^A) produced only dominant red sons and chocolate daughters (table 1, 1), which is as expected. Homozygous dominant red males mated with chocolate females, $B^AB^A \times b-$, produced all dominant red offspring, of both sexes (table 1, 3), which is again in agreement with expectation. Heterozygous dominant red males, having one chocolate parent, mated with chocolate females ($B^Ab \times b-$) produced dominant red and chocolate offspring of both sexes (table 1, 2) in approximately equal numbers.

If the gene for dominant red and the gene for black or chocolate were at separate loci on the chromosome, crossovers would be expected to appear among progeny from the last mentioned type of mating. The dominant red males used in these matings were produced by parents one of which was dominant red and the other chocolate. The dominant red parent, as previously explained, would have carried *B*, the gene for black, if both B^A and *B* could have been present on the same chromosome. There was no chocolate in the original dominant red parent stock. These males, phenotypically dominant red but having one chocolate parent, would be represented by the formula, *BA.ba*, if *B* and *A* were at separate points on the chromosome. Such males, mated with chocolate females, would be expected to produce the two parent phenotypes, *BA*, dominant red, and *ba*, chocolate, and two crossover types, *Ba*, black and *bA*, which presumably would be dominant red. The dominant red crossover type likely would be easily confused with the dominant red parent type. It might be impossible to distinguish between them phenotypically. But the other crossover type, black, would be readily detected should any such birds appear. No black offspring occurred among a total of 202 backcross progeny.

Dominant red males, heterozygous for black, mated with chocolate fe-

males ($B^4B \times b-$) produced dominant red and black progeny of both sexes (table 1, 4). The numbers secured are not large, only 36, and the proportion of dominant red to black is rather far from equality, but the types secured are as expected. At least one black male from among these progeny, when mated with a chocolate female, produced chocolate offspring, which would be expected.

In view of the rather complete discussions of the relation between dominant red and black already reported (COLE and KELLEY 1919) no more will be said of it here. The only change suggested is that dominant red be considered the allelomorph of black instead of epistatic to black.

Dominant red, black, and chocolate in relation to intensity

COLE and KELLEY (1919) have reported 39.72 percent crossing over between B^A[3] and I. Only a few matings have been made to study linkage between these two genes during the course of the present work, but additional data may be had from matings which happened to be suitable. These data are combined with those of COLE and KELLEY in table 2. The fact that their study was of dominant red and black with intensity while the present experiment concerns dominant red and chocolate with intensity should make no difference in combining the data, because the study in both cases concerns linkage of dominant red with intensity.

The double heterozygous males used in this portion of the experiment were all from intense dominant red females and chocolate males known to be heterozygous for intensity. Accordingly, they would be $B^AI.bi$,[4] and parent types among the progeny would be phenotypically B^AI, dominant red, and bi, dilute chocolate. Crossover types would be B^Ai, dominant yellow, and bI, intense chocolate. These data actually show an excess of crossovers, the total crossing over amounting to 59 percent.

When these are added to the data of COLE and KELLEY (table 2) the linkage value between B^A and I is changed from 39.72 to 47.01. Their statement, "Although with such small numbers a few records one way or the other may change the percentage value considerably . . . . " shows that they considered the value which they secured only tentative. Indeed the same might be said of the new value, 47.01, since the numbers have been increased over their 73 to only 117. These two points are widely separated on the sex chromosome, as measured by the frequency of crossing

[3] COLE and KELLEY used the symbol A for dominant red. B^A is being used here to designate the same gene.

[4] These males produced dilute colored offspring and hence were known to carry i.

TABLE 2

Showing linkage of I and B^A.

TYPE OF MATING		OFFSPRING			
		Non-crossover		Crossover	
Mating Number	Formulae of Parents ♂ × ♀	*BI*	B^Ai	B^AI	*Bi*
1365	$BI \cdot B^Ai \times Bi \cdot - -$	1	0	2	0
1456*	$B^Ai \cdot BI \times BI \cdot - -$	2	1	1	1
1523	$B^Ai \cdot BI \times Bi \cdot - -$	5	1	3	3
		B^AI	*Bi*	*BI*	B^Ai
1320	$B^Ai \cdot BI \times Bi \cdot - -$	0	2	0	1
1329*	$B^Ai \cdot BI \times B^AI \cdot - -$	0	1	0	0
1450	$B^Ai \cdot BI \times Bi \cdot - -$	2	0	0	0
1511	$B^Ai \cdot BI \times Bi \cdot - -$	5	4	3	2
1512	$B^AI \cdot Bi \times Bi \cdot - -$	4	0	2	0
1580	$B^AI \cdot Bi \times Bi \cdot - -$	2	2	0	1
1602	$B^AI \cdot Bi \times Bi \cdot - -$	6	1	3	4
1617	$B^AI \cdot Bi \times Bi \cdot - -$	1	1	2	1
1620	$B^AI \cdot Bi \times Bi \cdot - -$	1	0	0	0
1624	$B^AI \cdot Bi \times Bi \cdot - -$	1	1	0	0
Totals	COLE AND KELLEY (1919)	30	14	16	13
		B^AI	*bi*	*bI*	B^Ai
2386*	$B^AI \cdot bi \times bI \cdot - -$	0	1	1	2
2389*	$B^AI \cdot bi \times bI \cdot - -$	1	0	4	0
2391*	$B^AI \cdot bi \times bI \cdot - -$	1	0	1	3
2393*	$B^AI \cdot bi \times bI \cdot - -$	3	1	2	0
2431	$B^AI \cdot bi \times bi \cdot - -$	0	0	0	1
2439	$B^AI \cdot bi \times bi \cdot - -$	0	0	0	1
2442	$B^AI \cdot bi \times bi \cdot - -$	3	0	0	1
2444	$B^AI \cdot bi \times bi \cdot - -$	1	1	1	2
2447	$B^AI \cdot bi \times bi \cdot - -$	0	0	4	0
2449	$B^AI \cdot bi \times bi \cdot - -$	3	1	0	1
2452	$B^AI \cdot bi \times bi \cdot —$	0	2	2	0
Total this experiment		12	6	15	11
Total both experiments		42	20	31	24

Summary: 62 non-crossovers, 55 crossovers Percent crossing over, 47.01

Note: Matings numbered 1320 to 1624, inclusive, taken from COLE and KELLEY (1919).

* Only female offspring considered.

over; in fact, if it were not that both are sex linked, linkage between them would scarcely be suspected.

Matings were made to determine the linkage between *B* and *I*, B^A being excluded from this portion of the experiment (table 3). The heterozygous *Bi.bI* males used here had one dilute black parent, and the other intense chocolate. Parent phenotypes among the progeny were *Bi*, dilute black,

TABLE 3

Showing linkage of B and I.

PARENTS		OFFSPRING			
Mating Number	Formula ♂×♀	Non-Crossover		Crossover	
		Bi	*bI*	*BI*	*bi*
2323*	*Bi*·*bI*×*Bi*·– –	..	1	1	..
2377	*Bi*·*bI*×*bi*·– –	2	5	4	4
2382	*Bi*·*bI*×*bi*·– –	6	5	2	4
2390	*Bi*·*bI*×*bi*·– –	3	2	5	3
2394*	*Bi*·*bI*×*bI*·– –	1	7	1	2
2398	*Bi*·*bI*×*bi*·– –	4	2	2	3
2428	*Bi*·*bI*×*bi*·– –	1	3	1	1
2435	*Bi*·*bI*×*bi*·– –	2	..	1	2
2441	*Bi*·*bI*×*bi*·– –	1	..	..	4
2446	*Bi*·*bI*×*bi*·– –	..	1	2	3
2455*	*Bi*·*bI*×$B^A i$·– –	1	..	..	1
2456	*Bi*·*bI*×*bi*·– –	3	..	3	..
2459	*Bi*·*bI*×*bi*·– –	..	1	1	..
Totals		24	27	23	27

Summary: Non-crossover 51
Crossover 50
Percent crossing over 49.50

* Only female offspring considered.

and *bI*, intense chocolate. *BI*, intense black, and *bi*, dilute chocolate would be crossover types. There were 51 non-crossover progeny and 50 crossover progeny produced from such backcross matings. This would be expected in a case of independent assortment of *B* and *I*, so that here as with B^A and *I* no linkage could be postulated were it not that *B* and *I* are both sex linked.

The approximate correspondence of linkages between B^A and *I* and *B* and *I* (47.01 and 49.50 respectively), together with the fact that no crossing over between dominant red and chocolate occurred in a total of 202 backcross progeny, is strong evidence that genes B^A, *B*, and *b* are all at the same locus on the chromosome. If this is true then the data of tables 2 and 3 can be combined. Such combination shows 113 non-crossovers and 105 crossovers, or 48.12 percent crossing over between B^A and *I*, which may be taken as the present tentative value.

CHRISTIE and WRIEDT (1923) calculated 27.4 percent crossing over between B^A and *I*, but their numbers were small and their method of calculation very indirect. Omitting then their figures, the available linkage data on sex-linked characters in pigeons at the present time may be summarized as follows:

Genes	*Non-crossovers*	*Crossovers*	*Percent crossing over*	*Authority*
$I-B^A$	44	29	39.7	COLE and KELLEY (1919)
	18	26	59.0	HAWKINS (this paper)
	62	55	47.0	
$I-B$	80	46	36.5	STEELE (1931)
	51	50	49.5	HAWKINS (this paper)
	131	96	42.3	
B^A-B	202	0	0.0	HAWKINS (this paper)

It will be noted that for both the I-B^A and I-B linkages a higher percentage of crossovers was found by the present writer than by the previous investigators. In the I-B^A test the crossovers in fact considerably exceed the non-crossovers. The reason for this difference is not apparent; it can scarcely be attributed to differences in the stock used since for the most part the birds were from the same sources. Considering the fact that the two regions concerned are apparently so far apart, together with the difficulties involved in securing adequate numbers, the approximate equality of the values for the I-B^A and I-B linkages may be taken as consonant with the lack of crossing between B and B^A, thus supporting the interpretation that these two genes are really allelomorphs.

Black and chocolate flecking

COLE and KELLEY (1919) reported the occurrence of black flecking "in some of the (dominant) reds and apparently all of the gray birds" in their experiments.

One form of black flecking has been reported by WRIEDT and CHRISTIE (1925) as sex linked, due to a single dominant sex-linked gene, S_l. It occurs in both male and female birds. STEELE (1926), discussing the form of black flecking which occurs in dominant red and gray birds, distinguishes between this flecking, which is the type observed by COLE and KELLEY, and that reported by WRIEDT and CHRISTIE. Observations in the present experiment support STEELE's distinction.

STEELE says: "Flecks are intense black in the male, but dunnish or very subdued black in the female (considering only intense birds because differences are less striking in dilute types)."

Further observation of this kind of flecking has suggested a possible explanation of its inheritance. This explanation is not considered definitely established but rather as a working hypothesis. It is: That flecking is merely a result of a heterozygous condition; that dominant red or gray

males heterozygous for black or chocolate, B^AB or B^Ab, have black or chocolate flecks according to which recessive gene they carry, that homozygous dominant red birds, B^AB^A, are not flecked with black or chocolate; and that dominant red or gray females are never flecked with black or chocolate. Evidences supporting this hypothesis are:

1. Of the 30 or more flecked males which have been tested all have proved to be heterozygous, those with black flecks being B^AB and those with chocolate flecks B^Ab.

2. The non-flecked red and gray males tested have all proved to be B^AB^A.

3. Non-flecked red and gray males mated with black females produced sons all of which had black flecks.

4. Non-flecked red and gray males mated with chocolate females produced sons all of which had chocolate (not black) flecks.

5. No females have been observed which were definitely flecked with black or chocolate. Dark brownish red flecking appeared in some but this is considered to be caused by red pigment.

6. Non-flecked B^A females mated with black males produced sons all of which had black flecks.

7. Non-flecked B^A females mated with chocolate males produced sons all of which had chocolate flecks.

8. Flecked B^AB males, mated with black and chocolate females, produced sons all of which had black or chocolate flecks if they were B^A. Some, of course, were BB or Bb.

The statement of COLE and KELLEY (1919) that "apparently all of the gray .... birds show black flecks" may be explained on the basis that at that early date all their gray males were heterozygous for black. Any flecks which may have been present in females were probably dark red. The same would be true in the case of STEELE's observations.

The kind of flecking involved here is certainly different from that caused by the S_i factor of WRIEDT and CHRISTIE, unless it be assumed that S_i was contributed by the black or chocolate parent in every case where non-flecked B^A birds were mated with black or chocolate birds, and flecked sons were produced. The factor S_i, being dominant, could not have come from the B^A parent else that parent would have been flecked.

Black flecking in certain sub-varieties of pigeons has been regarded as a secondary sexual character (DARWIN 1875, GHIGI 1908, STEELE 1926) because it is found in the male only. GHIGI noted a marked sexual dimorphism in the flecking of certain species, particularly in "*Gazzi magnani.*" His descriptions, however, indicate the flecking observed by him to be

much more pronounced than that herein reported. The birds he described were in some cases largely black, whereas in this experiment flecked birds all have black or chocolate flecks on a red or gray background. GHIGI's descriptions resemble those of WRIEDT and CHRISTIE in this respect.

If black flecking were a secondary sexual character the testicular hormone would presumably be the primary factor in causing its expression. In order to ascertain whether the sex hormone is influential in this connection, six black-flecked B^A males of varying ages were bilaterally castrated. The plan was to pluck feathers following castration and observe whether new ones produced in their place were flecked. The results are summarized in table 4.

TABLE 4

*Showing results of castrating black-flecked males.**

BIRD	AGE AT CASTRATION	INTERVAL BETWEEN CASTRATION AND FIRST PLUCKING	INTERVAL BETWEEN CASTRATION AND LATER PLUCKING	FLECKING OF NEW FEATHERS	POSTMORTEM
Number	Months	Days	Days	Present or absent	Gonads
2387R	2 ⅔	6	39	Present	Gonads cleanly removed
2387N	5 ⅔	6	39	Present	Gonads cleanly removed
2437G	5 ⅓	6	39	Present	Gonads cleanly removed
2433F	4 ⅔	6	39	Present	Gonads cleanly removed
2433E	4 ⅔	4	39	Present	Very small bit of yellow tissue in left gonad region; right side clean
2364A	20	4	39	Present	Very small bit of yellow tissue in left gonad region; right side clean.

* All birds castrated April 11, 1930. Killed and examined 39 days later.

It was thought advisable to allow a lapse of a few days following castration before feathers were plucked in order that any testicular hormone present in the bird's body might be utilized or excreted. MORGAN (1915) and ROXAS (1926), working with Sebright bantams in which the male is normally hen feathered, castrated henfeathered cockerels and deplumed certain areas immediately. The new feathers which came in place were of the male type in form and color, suggesting that the influence of the testicular hormone upon the plumage ceased immediately after castration. The six males indicated in table 4 ranged from 2 ⅔ to 20 months of age when they were castrated on April 11, 1930. The male pigeon is sexually mature at about four months of age. Five of these males had well developed gonads. One, 2364A, had been mated over a year. The youngest male, 2387R, about 80 days old at the time, was sexually immature, and had very small

gonads. Black flecks were very evident in his plumage, however. The flecking becomes much more pronounced with successive molts, a condition also observed by WRIEDT and CHRISTIE (1925) in their birds.

Feathers with black flecks were plucked from two of the birds, 2433E and 2364A, four days after castration. Feathers were plucked from the other four birds six days after castration. Definite record of the exact feathers plucked was kept, and these feathers were preserved for comparison with those which should come in their place. The first feathers to come in after castration were those in the area surrounding the incisions. These were unmistakably flecked with black.

The new feathers began to emerge from their sheaths by the end of three weeks after castration. These feathers were definitely flecked with black, to as great a degree as their predecessors. Photographs of some of the birds were made thirty-three days after castration (figures 1, 2, and 3).

Close examination on May 20, 1930, thirty-nine days after castration, showed that in three of the six birds other feathers than those plucked had molted, later than the time of plucking, and new feathers were appearing in these follicles. These new feathers could not have been more than three weeks old, and since castration had occurred over six weeks previously, at least three weeks must have elapsed between castration and the beginning of their development. These new feathers were distinctly flecked, also. New feathers, corresponding to the ones plucked soon after castration, and some of these still younger feathers, were plucked on the same day, May 20. Figures 5 to 10 inclusive show all these feathers. By direct comparison it may be seen that the feathers produced after castration are as definitely flecked as those grown before castration. The six males were killed and examined on May 20 to ascertain whether a clean castration had been made. Four had no testicular tissue at all; a very small bit of tissue, yellowish in appearance, was found on the left side of each of the other two. This may have been a remnant of the left gonad.

Removal of the gonads in this experiment had no apparent effect upon either the kind or degree of flecking produced. The testicular hormone apparently is not, therefore, an appreciable factor in the production of fleck ing.

It was suggested that chocolate and black flecking have a bearing upon the hypothesis that B^A, B and b constitute a series of multiple allelomorphs. As already stated the mating of chocolate males with dominant red females for the production of heterozygous male offspring would be represented as ♂ *ba.ba* × ♀ *BA.*— if two separate loci on the chromosome were involved. The F_1 males would then be *BA.ba*, and any flecks they might

show should be black, because *B* is dominant to *b*. But all such F_1 males have not black but chocolate flecks. If these F_1 males are considered as being $B^A b$ any flecks appearing would be expected to be chocolate, because only genes for dominant red and chocolate are present. The males with black flecks are represented as $B^A B$ according to this scheme. This interpretation seems to satisfy the conditions observed during the course of this experiment.

Microscopic study of pigments

Numerous microscopic studies of pigments in the domestic fowl and the pigeon have been made by various workers, the most thorough of which, perhaps, is that of LLOYD-JONES (1915). His observations of the pigeon were mostly confined to various forms of black and recessive red. Physical differences between the relative number and arrangement of pigment granules in the feathers of different colored birds, described by him, offer explanation for the different optical effects. An attempt has been made to determine, if possible, whether dominant red and chocolate conform closely to the situation found in black.

Material used consisted of mature feathers plucked from certain definite parts of the bodies of live birds, whose colors were carefully described and whose breeding was known. The portion of the feather to be examined was removed with scissors, mounted in glycerin under a cover slip, and examined under both medium and high magnification. Most of the records were made from the 1.8 mm oil immersion objective. Transmitted daylight was the only type of illumination used for the recorded observations. This was found to be much more satisfactory than artificial light, particularly better than the sub-stage lamp, because there was less refraction of light, and individual pigment granules were much more clearly defined. These conditions for microscopic study, though extremely simple, proved quite satisfactory for the purpose. Not only could the color, relative density, and distribution of pigment be seen, but the individual granules could be observed and their size measured.

Black series

LLOYD-JONES (1915), in describing individual pigment granules of the black pigeon, says the color may be thought of as "attenuated black" or dun. A similar statement is made by WRIGHT (1917) when he says in regard to the black in mammals, "The pigment granules in this case are not really black but dark sepia brown."

The feathers of black birds are richly supplied with pigment. The pigment granules are fairly evenly distributed and so densely packed that

very little light can penetrate, resulting in a distinctly black optical effect. LLOYD-JONES (1915) states that the form of black granules varies considerably in different birds, one type being spherical, about 0.5μ in diameter, and another rod-shaped, about 0.8 to 1.5 μ long and 0.2μ in diameter. Most birds, according to him, possess both spherical and rod-shaped granules, usually with a preponderance of one or the other type.

Dilute black or dun feathers have the same kind of pigment as intense black but differ from the latter in quantity of pigment. The granules are fewer and more sparsely distributed in dun, which accounts for the true sepia color. Size and shape of the granule in dun are essentially the same as in intense black.

The common blue pigeon differs from black mostly in the manner of distribution of pigment. The granules are of the black type but in blue areas of the feather; they are clumped into groups, with intervening spaces which are void of granules. The "blue" color is due to this alternate arrangement of pigment clumps and blank spaces, in association with the keratin material of the feather. Black areas such as the wing bars of the blue pigeon have the pigment evenly distributed and the granules densely packed as in uniform black feathers. According to LLOYD-JONES (1915), the pigment granules in blue feathers are always spherical in shape and larger than those in black, 0.8μ – 1.0μ in diameter, and sometimes reaching a diameter of 2.0μ. The neck feathers in particular show very large, clearly spherical granules. Just what relation, if any, this bears to the metallic colors of this region is not known.

Dilute blue or silver bears the same relation to blue that dun bears to black. The difference, apparently, is one of amount rather than kind or distribution of pigment.

The work of LLOYD-JONES is much more complete but in so far as the present investigations have been carried the results are for the most part in keeping with his.

Dominant red series, and gray

Dominant red follows black closely in size and distribution of pigment granules in the various color patterns. The pigment in this group is distinctly reddish in color. The literature seems to afford no record of microscopic study of dominant red, except where it may have been included in examination of recessive red. LLOYD-JONES (1915, p. 462) describes a "plum color" as characteristic of certain areas, particularly the breast, and belly of some birds, and says the granules are spherical and remarkably large in size, "often reaching 2.5μ to 3.0μ in diameter." It is possible he

may have been describing a dominant red. The pigment granules of a dominant red barred bird are spherical and very large in the neck region, although diamenters of 1.3 to 1.5μ are the largest observed in this work.

Pigment granules in the dominant red feather are spherical in shape, about 0.8μ in diameter, and evenly distributed throughout the barb and barbule. This type of granule is found in all the red areas of the body.

Dominant yellow, the dilute form of dominant red, is distinctly yellow in color, and the pigment is less completely divided into granules than the intense pigment. Dominant yellow is closely comparable to recessive yellow under the microscope. The statement of LLOYD-JONES (1915) that yellow pigment exists as irregular formless clumps, or agglomerations is partially borne out by these studies. Finely divided granules, spherical in shape, approximately 0.3μ in diameter, have also been seen in both recessive and dominant red, which is slightly different from his findings. He was unable to distinguish individual granules. LADEBECK (1923) also observed yellow pigment in certain domestic fowls only in a diffuse form.

Pigment granules in the dominant red barred bird are large in the iridescent areas about the neck and breast, spherical in shape, 1.2μ to 1.5μ in diameter, and clumped as in "blue." They are distinctly red in color and densely packed together in the intense form.

Dominant yellow barred is characterized by the same kind of pigment as dominant yellow, but there is more tendency toward clumping than in uniform yellow. The wing-bows often are practically devoid of pigment, only occasional clumps being present. Granules are much more numerous in the wing bars, of course, where the effect is much the same as in uniform yellow.

The gray of the slaty rump, tail, and primaries of dominant red birds, and of the entire body of uniformly gray birds is characterized by a distinctly granular type of pigment, but individual granules are less deeply colored than those in black and red. Granule shape and size are quite similar to that found in black, namely, spherical, and varying from 0.4μ to 0.6μ in diameter. The granules are more sparse in gray than in black or red.

Red, black, or chocolate in gray feathers, present in the form of "mealiness" and flecks, exists as aggregations of pigment granules which are typical in size, shape, and color for the kind of pigment concerned(red, black, or chocolate).

Chocolate series

Chocolate color is produced by pigment granules which are deep brown in color, spherical in the samples examined, and somewhat smaller than black.

Dilute chocolate, or drab, has essentially the same kind of pigment, but the granules are fewer than in the intense form.

Brown silver, the intense type analogous to blue barred and dominant red barred, possesses chocolate or brown colored pigment. The granules are smaller than black (blue) in the samples observed, but are clearly defined. They are spherical in shape, and clumped as in blue.

It is difficult to see the pigment in drab silver except in the heavier pigmented areas. Widely scattered granules may be found in such light areas as the wing bows and back, however. The pigment is chocolate colored, but the granules are so sparse that the bird is very light in color.

These microscopical studies have revealed a similarity of dominant red and chocolate to black in the matter of distribution of pigment granules in the feather. This type of red was found also to resemble black closely in form and size of pigment granule. Chocolate granules, in general, were observed as slightly smaller than either black or dominant red. The pigment of gray birds is granular the same as black, red, and chocolate, but these granules are usually very light in color.

GENERAL REMARKS

COLE (1914) and WRIGHT (1917) have considered red as a fundamental pigment, potentially present in all birds and mammals. WRIGHT (1917) postulates the existence of two enzymes, designated by him as enzyme I and enzyme II, which, by acting upon a chromogen, produce different colored pigments. Enzyme I oxidizes the chromogen to red. Enzyme II is supplementary to enzyme I, and is effective only in combination with it. Enzymes I and II together oxidize the chromogen to sepia (black). In order to account for an intermingling of red and black granules, WRIGHT suggests a mere reduction in quantity of enzyme II, red or black being formed as one or the other of the respective enzymes chances to predominate. Chocolate pigment is accounted for by him as "a uniform reduction in potency (of enzyme II) in some other way not involving a reduction in quantity."

COLE and KELLEY (1919) suggest the primary action of gene B^4 (their A factor) to be a modification of black rather than the direct production of red pigment. Microscopic studies, as well as macroscopic observations, suggest a close similarity between dominant red and recessive red pigment. The type of red referred to by WRIGHT as produced by the action of enzyme I on the chromogen is recessive to black and chocolate. Breeding results indicate that the dominant red pigeon possesses all the genes necessary for the production of black or chocolate pigment, but has the gene

B^A in addition. Since dominant red pigment resembles recessive red in appearance B^A may be thought of as an inhibitor of black or chocolate pigment. B^A then is to be regarded as an inhibitor of WRIGHT's enzyme II.

Although WRIGHT put chocolate and black pigment in the same class, there would appear to be a real difference between them. It therefore is not only convenient, but would appear appropriate, to separate WRIGHT's enzyme II into two entities, on the basis of their action. These may be designated II and II′, respectively. On this assumption II (in conjunction with the chromogen and enzyme I) would produce chocolate pigment, whereas II′ under the same conditions would give black. The situation in pigeons may then be interpreted on this basis.

In the absence of extension (that is, in *ee* birds) the feathers have only the chromogen and enzyme I, which results in hypostatic (recessive) red. We shall then have the following series, B^A being defined as a gene which inhibits the action of the second enzyme (both II and II′), but not enzyme I:

ee (B^A, *B* or *b*), chromogen plus I gives hypostatic red.

E bb, chromogen plus I plus II gives chocolate.

E BB (or *Bb*), chromogen plus I plus II′ gives black.

E B^AB^A, chromogen plus I plus II (or II′) plus inhibitor gives dominant red, without flecks.

E B^Ab, chromogen plus I plus II plus inhibitor gives dominant red, but in heterozygous condition B^A is not complete in its action; small areas are left under the influence of II and constitute chocolate flecks.

E B^AB, chromogen plus I and plus II′ plus inhibitor gives dominant red with areas affected by *B* and hence with black flecks.

Since B^A affects only II (or II′) it is to be expected that the dominant red portions would be subject to those factors governing the distribution of black and chocolate (for example the *S*—series), as is found to be the case (red check corresponding to black check, red-barred corresponding to black-barred blue, etc.).

There would be a certain logical advantage in regarding dominant red as due to the two genes, *B* and *A*, completely linked, rather than as a single gene, B^A. Dominant red birds are never uniformly red throughout, but always have a certain amount of gray or slatiness as already described. Such a *BA* arrangement might seem to account better for the presence of a pigment other than red. It might seem on first thought that the presence of two genes, *BA*, completely linked, would better explain the black flecked also. This would seem especially logical if homozygous dominant red birds were flecked. But the indication is, however, that flecked birds

are always heterozygous for dominant red, and the black of the flecks is accounted for by the presence of one gene for black as the allelomorph of the one which produces red. Difficulty is encountered in explaining the presence of chocolate flecks in males which would have the formula *BA.ba* if *B* and *A* are non-allelomorphic genes. *B* is known to be dominant to *b;* and such males should show only black flecks, but in this experiment all of them have not black but chocolate flecks. The existence of an additional inhibitor of *B*, permitting *b* to express chocolate, would have to be assumed to account for this result. Considering this and the fact that no crossing over between dominant red and chocolate occurred the interpretation that B^A, *B*, and *b* constitute a series of allelomorphs, rather than that there are two separate completely linked genes for each color, seems best to account for the observed facts.

The optical effect produced by B^A supports, to some extent at least, the theory recently advanced by FISHER (1928) regarding the possible modification of the response of the wild type to recurrent mutations, and the origin of dominance. B^A, even in the homozygous condition, produces a bird not entirely red, for there is always an appreciable amount of slate color in the wings, rump, and tail. Neither is B^A completely dominant to *B* and *b*, for heterozygous B^AB and B^Ab birds show varying amounts of black and chocolate respectively. It may be that B^A is a relatively new mutation from *B* and that later modifications will render it completely dominant to its allelomorphs.

RAPER (1927) produced a red substance by permitting tyrosinase to act on 3, 4 dihydroxyphenylalanine, $(HO)_2.C_6H_3.CH_2.CH(NH_2).COOH_2$. This red substance was allowed to decolorize (in air), and 5, 6 dimethoxyindole was isolated from the resulting products. This same indole was produced from tyrosine. RAPER further states:

"5,6 dihydroxyindole and 5, 6 di-hydroxyindole-2-carboxylic acid have been identified as products of the action of tyrosinase on tyrosine and are to be regarded as the immediate precursors of melanin.

"3, 4 dihydroxyphenylalanine gives rise to 5, 6 dihydroxyindole under the same conditions that result in its production from tyrosine. This confirms the previous suggestion that 3,4 dihydroxyphenylalanine is the first immediate product in the tyrosinase-tyrosine reaction.

"The formula previously given to the red pigment produced from tyrosine has been revised in view of further evidence presented in this paper. It is probably the 5, 6 quinone of di-hydroindole-2-carboxylic acid."

Lack of sufficient experimental evidence to bridge the gap between the

work of RAPER, and other chemists, and that of geneticists studying color inheritance forbids any positive conclusions here. It may be true, however, that the red pigment produced by the action of tyrosinase on tyrosine is similar to the red pigment of birds and mammals. The identification of these intermediate products may prove helpful in further study of the chemistry of animal pigments.

SUMMARY

1. Dominant red, black and chocolate pigmentation in the domestic pigeon are regarded as an allelomorphic series, and evidence is put forth to support the hypothesis.

2. Linkage values between dominant red and intensity and chocolate and intensity are shown to be essentially the same.

3. No crossover types, between dominant red and chocolate, were secured in 202 backcross offspring.

4. Chocolate and black flecking in dominant red and gray birds is considered to exist only in males which are heterozygous for dominant red, either $B^A B$ or $B^A b$.

5. Evidence is offered to show that flecking is not a secondary sexual character, due primarily to the sex hormone.

6. Gene B^A changes both B and b to dominant red, but in the heterozygous condition its action, as regards feather area, is not quite complete.

7. The dominant red and chocolate series are homologous to the black series in the size, shape, and arrangement of pigment granules, as also with respect to factors modifying the distribution of the pigment.

8. The biochemical relations of pigments in the tyrosinase-tyrosine reaction, so far as they are understood, give some promise of confirming a direct biochemical relationship between genes for color and pigment formation in birds and mammals.

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FIGURE 1.—2364A–B^AB gray with black flecks, 33 days after castration; arrows indicate new feathers.

FIGURE 2.—2433F–B^AB dominant red with black flecks 33 days after castration; arrows indicate new feathers.

FIGURE 3.—2433E–B^AB gray with black flecks, 33 days after castration; arrows indicate new feathers.

FIGURE 4.—2330L–B^Ab dominant red with chocolate flecks; not castrated.

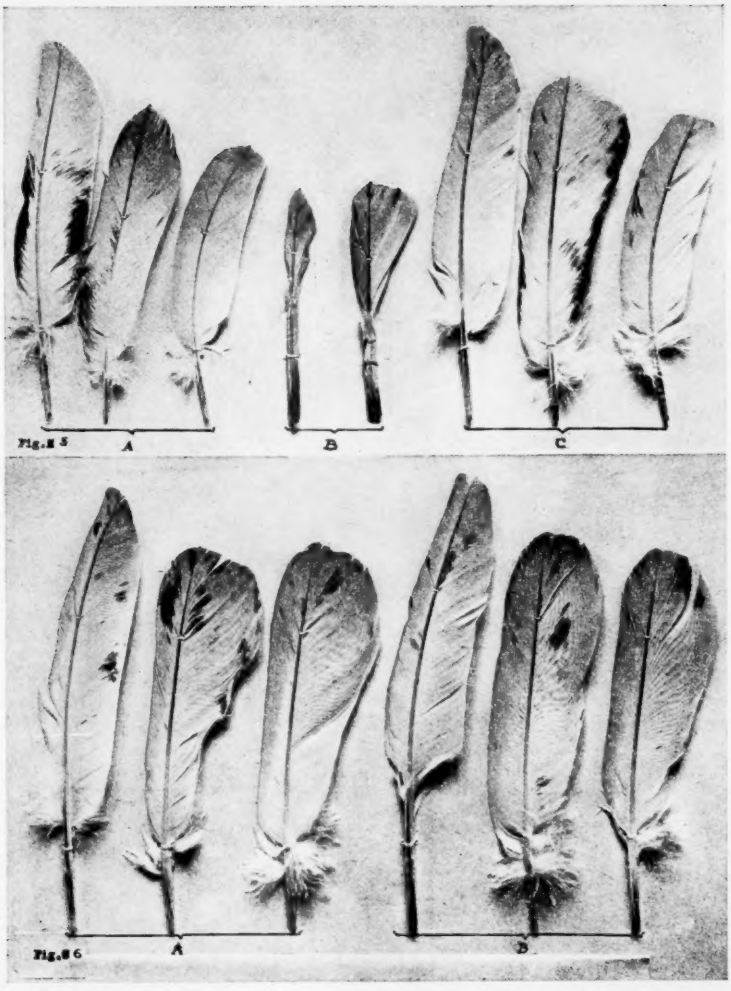

FIGURE 5.—2387R. A, feathers plucked 6 days after castration. B, very young feathers 39 days after castration. C, feathers corresponding to A, 39 days after castration.

FIGURE 6.—2433F. A, feathers plucked 6 days after castration. B, feathers corresponding to A, 39 days after castration.

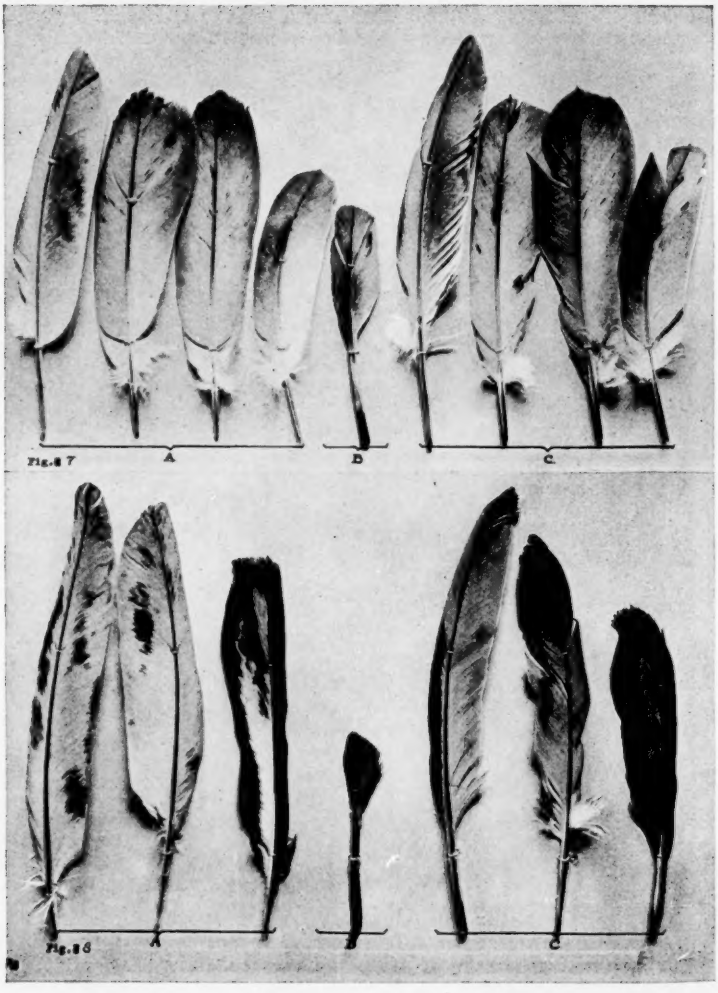

FIGURE 7.—2387N. A, feathers plucked 6 days after castration. B, very young feathers 39 days after castration. C, feathers corresponding to A, 39 days after castration.

FIGURE 8.—2364A. A, feathers plucked 4 days after castration. B, very young feather 39 days after castration. C, feathers corresponding to A, 39 days after castration.

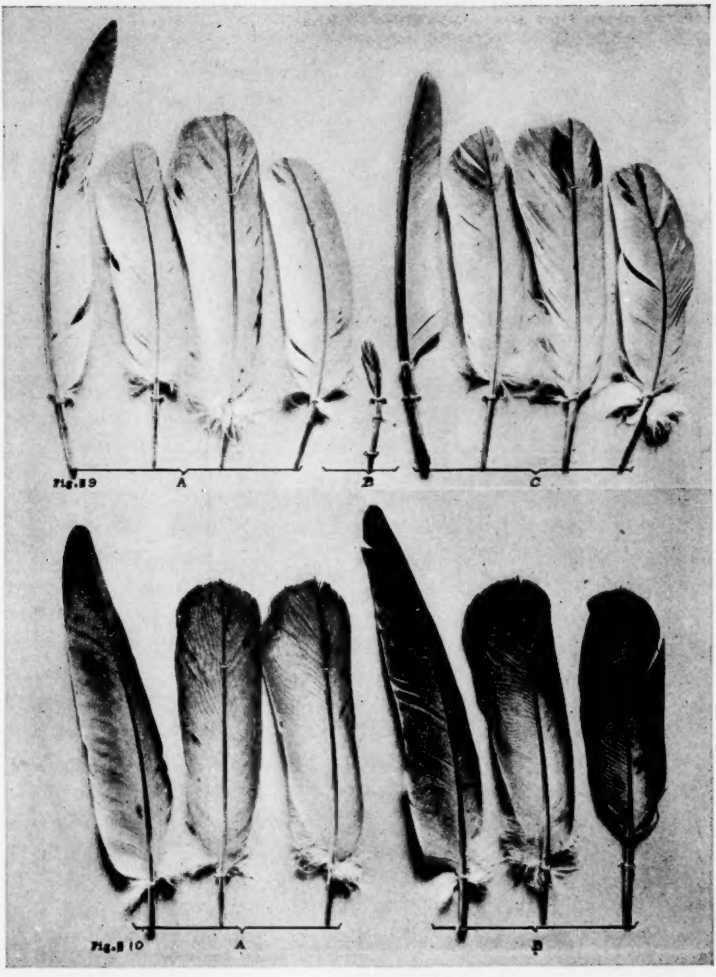

FIGURE 9.—2433E. A, feathers plucked 4 days after castration. B, very young feather 39 days after castration. C, feathers corresponding to A, 39 days after castration.

FIGURE 10.—2437B. A, feathers plucked 6 days after castration. B, feathers corresponding to A, 39 days after castration.

VIVIPARY IN MAIZE[1]

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INTRODUCTION

The continuous development of a plant body from its unicellular inception to maturity, without the intervention of a period of dormancy, is called vivipary. In viviparous plants, the embryos develop into seedlings even while the seeds are still contained in the fruits of the parent sporophyte. Similarly, spores may develop into gametophytes without undergoing a period of dormancy.

Viviparous maize plants were described in an earlier publication (EYSTER 1924a) under the name "primitive sporophyte." This name was suggested by the fact that the sporophytes of all non-seed-bearing plants, which presumably are more primitive than seed-bearing plants, are normally viviparous. Since "primitive sporophyte" as well as such terms as "defective kernel" and "premature germination," which have been used in referring to maize sporophytes that apparently do not undergo a dormant period, are ambiguous and misleading, it seems best to use the botanically correct term in describing this phenomenon, namely, vivipary.

Viviparous maize plants first occurred in pedigreed cultures grown at the UNIVERSITY OF MISSOURI Agricultural Experiment Station, and with few

[1] Contributions from the Botanical Laboratory of BUCKNELL UNIVERSITY. Paper number 1. The contributions which are to issue from the newly established Botanical Laboratory of BUCKNELL UNIVERSITY are made possible by the generosity of BUCKNELL UNIVERSITY in providing time and facilities for investigational work, and are dedicated to DOCTOR NELSON F. DAVIS whose unselfish interest and cooperation serve as a constant inspiration.

exceptions lacked completely the chloroplastid pigments. The close association between vivipary and albino seedlings was regarded by EYSTER (1924a) as being due to separate but closely linked genes, while MANGELSDORF (1926) prefers to believe that physiological correlation is a more plausible explanation of the absence of chloroplastid pigments in the viviparous plants. That linkage and not physiological correlation is responsible for the close relationship between vivipary and albinism was demonstrated by self-fertilizing a large number of plants heterozygous for vivipary and albinism. Among the many albinotic viviparous seedlings occurred a few green viviparous seedlings which have been regarded as crossovers. When these green seedlings were removed to the soil, they grew to maturity and gave rise to a chlorophyll-bearing strain of viviparous maize.

In another paper by EYSTER (1924b) it was shown that at least two genes induce vivipary in maize.

While the first of the above-mentioned papers was in press, descriptions of what appear to be vivipary in maize were published by LINDSTROM (1923) in a paper concerned with "Endosperm defects" and by MANGELSDORF (1923) as "Germinating seeds." According to MANGELSDORF, "germinating seeds" are characterized by the failure of the embryo to go into the resting stage. Since germination implies dormancy, it is obvious that "germinating seeds" does not correctly apply to the character described.

Later MANGELSDORF (1926) adopted the term "premature germination" and differentiated genetically different types largely on the basis of the stage of endosperm development at which germination begins. Just how it was determined when dormancy began and ended in each case, and that dormancy was not completely inhibited by the gene which is assumed to produce premature germination is not stated.

More recently MANGELSDORF (1930) has presented a more extensive study of "premature germination." To explain the numerical results observed in various stocks, fifteen genes have been called into service. The descriptions of the different types of "premature germination" are based entirely upon time of germination and the degree of development of the chloroplastid pigments. To what extent these differences may have been caused by other genes and by environmental factors does not seem to have been determined.

ORIGIN AND DESCRIPTION OF VIVIPARY IN MAIZE

Vivipary has occured in a number of different and unrelated strains of maize. No attempts have been made to determine the nature of the origin of vivipary in any of the strains.

So far as observations have been made, viviparous maize plants have a continuous development from the fertilized egg to the mature plant so that dormancy and germination are not involved. The development of the

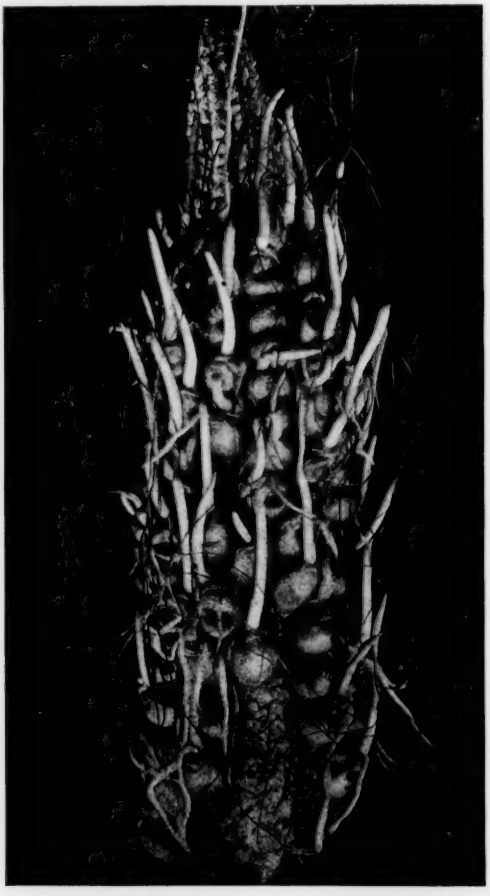

FIGURE 1.—An ear of maize homozygous for vivipary$_1$ showing the viviparous embryos in various stages of development.

chloroplastid pigments as well as other plant pigments is conditioned by other genetic factors in viviparous plants exactly as in non-viviparous plants. When viviparous seedlings of such genetic constitution that the

plastid pigments develop normally are transferred to soil, they develop into mature plants. A maturing ear of a homozygous viviparous plant is shown in figure 1. Although the embryos of all kernels are homozygous for vivipary, they are in different stages of development. Some of the em-

FIGURE 2.—Mature plants which are homozygous for $vivipary_1$.

bryos are hurrying into the seedling stage, while others are still so small that the kernels appear to contain non-viviparous embryos. It would be impossible to characterize vivipary in maize on the basis of a definite relationship between a stage in endosperm development and the appearance

of the plumule and radicle of the developing seedling as has been done by MANGELSDORF in differentiating the different types of "premature germination."

Viviparous maize plants have been growing continuously through consecutive generations, without a period of dormancy in the seed stage, for three years. The fourth continuous generation of viviparous maize$_1$ is shown in figure 2. These viviparous plants apparently grew as vigorously as non-viviparous plants belonging to the same strain.

INHERITANCE OF VIVIPARY IN MAIZE

Vivipary in maize is inherited as a simple Mendelian recessive character, and is brought into expression by a number of different genetic factors. The genes for vivipary which have been studied are indicated by the symbols V_{p1}, V_{p2}, V_{p3}, and V_{p4}. The effect of each of these genes is to inhibit dormancy and cause the sporophyte to undergo continuous development from the fertilized egg to the mature sporophyte, as is characteristic of the sporophytes of non-seed-bearing plants. The time of the appearance of the plumule and radicle outside of the pericarp varies with changes in the genetic constitution of the individual. Vivipary$_1$ has been studied in pure cultures and in various hybrid combinations, and it has been found that in some stocks the seedlings are quite large at the time of maturity of the ear, while in others they are so small that they often do not even burst through the pericarp at the time of kernel maturity.

In F_2 progenies segregating vivipary$_1$, 24026 kernels were classed as having normal and 8336 as having viviparous embryos. These results show a deviation of 220 ± 53 kernels from the expected frequencies. Backcross progenies involving vivipary$_1$ yielded 1709 kernels with normal and 1726 kernels with viviparous embryos. The deviation between the observed and expected frequencies in these backcrosses is 8.5 ± 51 kernels.

Vivipary$_2$

F_2 progenies segregated 2625 kernels with normal and 959 kernels with viviparous kernels. This is a deviation of 63 ± 17.5 kernels from the expected frequencies. Intercrosses between vivipary$_1$ and vivipary$_2$ yielded normal plants, which, when self-fertilized, produced normal and viviparous kernels in the relation of 9:7. These results indicate that vivipary$_1$ and vivipary$_2$ are caused by genes having their loci in different chromosomes.

Vivipary$_3$

F_2 progenies segregated 723 kernels with normal and 208 kernels with

viviparous embryos. This is a deviation of 25 ± 8.91 kernels from the expected frequencies.

Vivipary$_4$

Up to the present time a single F_2 progeny involving vivipary$_4$ has been studied. This progeny included 214 kernels with normal and 109 kernels with viviparous embryos. These results represent a deviation of 28 ± 6.85 kernels from the frequencies that were to be expected.

The identity of the different genes for vivipary has been determined by their linkage relations as is shown in a later section of this paper.

SPURIOUS RATIOS OF NORMAL VERSUS VIVIPAROUS KERNELS

The wide variation in the stage of development of the viviparous embryos at the time of the maturity of the ear as indicated by the hardened endosperm is due in part to inherent genetic factors and in part to external environmental factors, especially moisture. By harvesting homozygous viviparous ears prematurely and drying them by blowing air over them by means of an electric fan, it has been possible to induce some or all of the embryos of such ears to become dormant. So, also, when the maturing ears of normal strains of maize are exposed to abnormally moist conditions, there is a tendency for the embryos to continue their development. Whether the embryos actually undergo a period of dormancy under these conditions is an open question.

There appears to be a greater tendency for the kernels which are heterozygous for vivipary than for the homozygous normal kernels to germinate on ears which are maintained under moist conditions. Accordingly, when ears which are heterozygous for vivipary are exposed to moist conditions, there may be an excess of viviparous kernels due to the germination of some of the heterozygous kernels which, under drier conditions, would have remained dormant.

In the study of the effect of premature drying on viviparous embryos, *R*-testers homozygous for shrunken endosperm and vivipary$_1$ were used. The self-fertilized ears of these plants were harvested and dried while the kernels were still immature. Accidental contaminations by pollen from other plants in the field could be recognized by (1) non-shrunken endosperm, and (2) colored aleurone.

The self-fertilized ears of plants which are homozygous for vivipary$_1$ and the *R*-aleurone color factor and homozygous for the other genes necessary for the development of colored aleurone bear, with rare exceptions, normal kernels with colored aleurone and viviparous kernels with colorless aleurone. The recombinations of these characters, due to crossing over,

occurred with a frequency of less than two per thousand kernels. In the study of the effects of premature drying and of increased moisture, respectively, the colored kernels from the self-fertilized ears could be regarded as homozygous non-viviparous and heterozygous viviparous, while the colorless kernels were, with rare exceptions, homozygous for vivipary.

Induced dormancy of viviparous kernels under dry conditions and germination of normal kernels under moist conditions give rise to all sorts of numerical ratios between normal and viviparous kernels, even when vivipary_1 alone is concerned. The spurious ratios thus obtained varied from 328 non-viviparous :1 viviparous to 1 non-viviparous:2.3 viviparous kernels. These results emphasize the importance of exercising extreme caution in the liberal and wholesale assumption of multiple factors, with and without linkage, in explaining observed numerical relationships.

The viviparous kernels, which have been forced into dormancy by artificial drying, germinate when they are exposed to suitable growth conditions. A number of viviparous plants which had undergone a period of induced dormancy were grown to maturity and, when self-fertilized, produced viviparous kernels exclusively, thus showing that they actually were homozygous for vivipary_1.

In like manner, germinating kernels with colored aleurone in which vivipary was induced by maintaining the maturing ear under moist conditions were transferred to soil and the plants grown to maturity. The self-fertilized ears of these plants produced kernels with dormant and viviparous embryos in the relation of 3:1, thus indicating that vivipary had been induced in heterozygous plants.

SUMMARY OF GENES USED IN THIS STUDY

The genes referred to in this study belong to linkage groups as indicated below.

Group	*Gene*	*Character*
I	c	Colorless aleurone
	sh	Shrunken endosperm
	v_{p4}	Viviparous embryo
II	g	Golden plant
	r	Colorless aleurone
	v_{p1}	Viviparous embryo
III	su	Sugary endosperm
	v_{p3}	Viviparous embryo
V	P_l	Plant color
VIII	P_r	Purple aleurone
	r_{c1}	Reduced endosperm
	r_{c2}	Reduced endosperm
	sc_1	Scarred endosperm
	v_{p2}	Viviparous embryo
	Y_3	Yellow endosperm

SUMMARY METHOD OF PRESENTATION OF THE DATA

The data are presented in summary form only, and are grouped into tables, where possible, to save space. The detailed data are on file in the laboratory of the writer and will be furnished upon request.

LINKAGE RELATIONS OF VIVIPARY$_1$

The gene for vivipary$_1$ is very closely linked with the *R* aleurone color gene as shown by the data in table 1 and the illustration in figure 3.

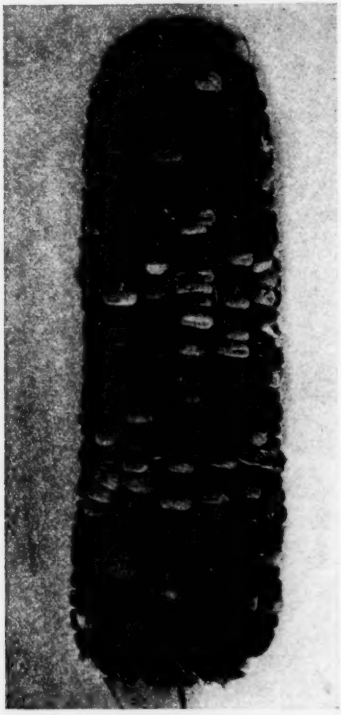

FIGURE 3.—A self-fertilized ear of a plant which was heterozygous for vivipary$_1$ and colored aleurone. Note that the colored kernels have dormant and the colorless kernels viviparous embryos due to the very close linkage between the *R*-aleurone color factor and the V_{p1} factor for vivipary.

Vivipary$_1$ and colored aleurone

Plants heterozygous for V_{p1} and *R* and homozygous for all other genes which are necessary for the development of colored aleurone were back-

crossed reciprocally with homozygous viviparous *R*-testers. The results of these backcrosses are given in table 1 A. Only 5 kernels among the 3435 which resulted from the backcrosses had the segregating characters in recombinations. These results indicate a linkage with 0.15 percent crossing over.

TABLE 1

Tests involving vivipary$_1$ and aleurone color factors.

PART	NATURE OF THE TESTS	COLORED ALEURONE		COLORLESS ALEURONE	
		V_{p1}	v_{p1}	V_{p1}	v_{p1}
A	Backcross involving *R* and V_{p1}	1707	3	2	1723
B	F_2 progenies involving *R* and V_{p1}	6070	23	19	2092
C	F_2 progenies involving *R*, *C*, and V_{p1}	5783	27	1871	2670
D	F_2 progenies involving *R*, *C*, *A*, and V_{p1}	5326	39	4957	3485

The close linkage shown by the backcross data is substantiated by F_2 data involving (1) *R* and V_{p1} as given in table 1B, (2) *R*, *C*, and V_{p1} as given in table 1C, and (3) *R*, *C*, *A*, and V_{p1} as given in table 1D.

Vivipary$_1$ and golden plant

According to LINDSTROM (1917, 1918), there is approximately 23 percent crossing over between *R* and *G*. As V_{p1} is very closely linked with *R*, it should show approximately the same linkage with *G* as *R* does.

As yet only limited data on the relationship between V_{p1} and *G* are available and are given in table 2A and B. The data in table 2A represent an F_2 progeny in the coupling series, while the data in table 2B represent a

TABLE 2

Further linkage tests involving Vivipary$_1$.

PART	PROGENY	FACTORS INVOLVED		*AB*	*Ab*	*aB*	*ab*	LINKAGE
		A	*B*					
A	F_2	*G*	V_{p1}	242	58	58	42	Yes
B	F_2	*G*	V_{p1}	40	28	28	0	Yes
C	F_2	S_h	V_{p1}	14043	4847	5090	996	No
D	F_2	S_h	V_{p1}	374	123	96	39	No
E	F_2	P_r	V_{p1}	959	0	352	0	No

repulsion series. These results indicate a linkage between V_{p1} and *G* with approximately 35 percent crossing over. The data here presented are too limited to be of value other than to substantiate the linkage which was to be expected.

Vivipary$_1$ and shrunken endosperm

The results of F_2 progenies which segregated vivipary$_1$ and shrunken endosperm are given in table 2C. There is a marked tendency for homozygous viviparous embryos to become dormant in the seed stage when the endosperm is homozygous shrunken, and this may be caused by a more rapid withdrawal of water from the embryo as the kernel approaches maturity. By allowing for the tendency of shrunken endosperm to inhibit vivipary, we find the data indicate that vivipary$_1$ and shrunken endosperm are inherited independently.

Vivipary$_1$ and sugary endosperm

Vivipary$_1$ is inherited independently of sugary endosperm as indicated by the F_2 data given in table 2D.

Vivipary$_1$ and purple aleurone

F_2 data on the relationship between V_{p1} and P_r are given in table 2E. Since all of the kernels which had viviparous embryos had colorless aleurone due to the very close linkage between V_{p1} and R, they could not be classified with respect to the P_r gene. The relation of P_r to p_r among the kernels which have non-viviparous embryos and colored aleurone indicates that P_r and V_{p1} are inherited independently.

LINKAGE RELATIONS OF VIVIPARY$_2$

Vivipary$_2$, so far as can be determined by ordinary observation, is phenotypically indistinguishable from vivipary$_1$ and is the expression of a gene in chromosome VIII.

Vivipary$_2$ and purple aleurone

The results from F_2 progenies which segregated viviparous embryos and red aleurone color are given in table 3A and B. *A* represents V_{p2} and P_r in

TABLE 3

Linkage tests involving vivipary$_2$.

PART	PROGENY	FACTORS INVOLVED		*AB*	*Ab*	*aB*	*ab*	LINKAGE
		A	*B*					
A	F_2	V_{p2}	P_r	269	66	47	24	Yes
B	F_2	V_{p2}	P_r	216	95	76	4	Yes
C	F_2	V_{p2}	R_{s1}	2058	190	252	620	Yes
D	F_2	V_{p2}	S_{s1}	300	21	16	68	Yes
E	F_2	V_{p2}	R_{s2}	257	0	4	72	Yes
F	F_2	V_{p2}	S_h	236	62	72	16	No
G	F_2	V_{p2}	Y_2	250	2	16	81	Yes

coupling series and B in repulsion series. These results indicate a linkage between V_{p2} and P_r with approximately 30 percent crossing over.

Vivipary$_2$ and reduced endosperm

Reduced endosperm$_1$ and reduced endosperm$_2$ are genetic variations in kernels of maize in which the amount of endosperm which is formed is greatly reduced, and are the expressions of genes which have their loci in chromosome VIII as shown by EYSTER (in press).

The results of F_2 progenies segregating vivipary$_2$ and reduced endosperm$_1$ are given in table 3C, and indicate a linkage between these characters with approximately 15.5 percent crossing over.

Vivipary$_2$ and reduced endosperm$_2$

F_2 progenies involving vivipary$_2$ and reduced endosperm$_2$ are given in table 3E. These data indicate a linkage between V_{p2} and R_{e2} with 1.2 percent crossing over.

Vivipary$_2$ and scarred endosperm$_1$

This pair of characters was found to be linked with 9.6 percent crossing over as shown by the F_2 data given in table 3D. This linkage is in agreement with the genetic correlation between S_{c1} and P_r previously reported by EYSTER (1926).

Vivipary$_2$ and shrunken endosperm

A single F_2 progeny which segregated vivipary$_2$ and shrunken endosperm indicates that the genes for these two characters segregate independently. The observed frequencies of this progeny are given in table 3F.

Vivipary$_2$ and yellow endosperm$_2$

One of the progenies which segregated normal and viviparous kernels also segregated yellow and white endosperm. A striking feature of this progeny was that practically all of the yellow kernels were non-viviparous while almost all of the kernels with white endosperm were viviparous, thus suggesting a linkage between the factors for vivipary and white endosperm. The F_2 data on this relationship, as given in table 3G, indicate a linkage between V_{p2} and Y_2 with approximately 5.3 percent crossing over.

Vivipary$_2$ and colored aleurone

F_2 progenies involving the R and C aleurone color factors and V_{p2} are given in table 4A, and others involving the A, R, and C aleurone color factors with V_{p2} are given in table 4B. These results indicate that V_{p2} is segregated independently of all aleurone color factors.

TABLE 4

F_2 progenies involving colored aleurone and various chromosome VIII characters.

PART	FACTORS INVOLVED		*AB*	*Ab*	*aB*	*ab*
	Colored Aleurone *A*	Chromosome VIII Character *B*				
A	*R* and *C*	V_{p2}	318	226	97	85
B	*A*, *R*, and *C*	V_{p2}	164	157	32	52
C	*A*, *R*, and *C*	S_{c1}	151	45	165	44
D	*A*, *R*, and *C*	Y_2	188	59	171	47

Scarred endosperm$_1$ and colored aleurone

One of the pedigrees which segregated for scarred endosperm$_1$ also segregated kernels with colored and colorless aleurone in the ratio of 27:37, thus showing that all three factors for aleurone were involved. The data, which are given in table 4C, indicate that S_{c1} segregates independently of the aleurone color factors.

Yellow endosperm$_2$ and colored aleurone

One of the progenies which segregated yellow endosperm$_2$ also segregated colored and colorless aleurone in the ratio 27:37, thus showing that the *A*, *C*, and *R* aleurone color genes had been involved. The observed frequencies, given in table 4D, indicate that yellow endosperm$_2$ is inherited independently of aleurone color.

Scarred endosperm and purple aleurone

The data given in table 5A, representing an F_2 progeny which segregated scarred endosperm$_1$ and purple aleurone, indicate a linkage between S_{c1} and P_r with approximately 20.7 percent crossing over.

Reduced endosperm$_1$ and shrunken endosperm

The F_2 data on this relationship are given in table 5B, and indicate that R_{c1} and S_h segregate independently. It is difficult to distinguish between non-shrunken and shrunken endosperm when the kernels are homo-

TABLE 5

Miscellaneous linkage tests involving chromosome VIII characters.

PART	FACTORS INVOLVED		*AB*	*Ab*	*aB*	*ab*	LINKAGE
	A	*B*					
A	S_{c1}	P_r	105	46	43	2	Yes
B	R_{c1}	S_h	939	294	346	66	No
C	R_{c2}	S_h	198	63	55	17	No
D	R_{c1}	Y_2	243	15	22	68	Yes

zygous for reduced endosperm$_1$. This difficulty is responsible for the wide deviation between the observed and expected frequencies of reduced kernels with non-shrunken and shrunken endosperm as given in table 5B.

Reduced endosperm$_2$ and shrunken endosperm

F_2 data showing that these two characters are inherited independently are given in table 5C.

Reduced endosperm$_1$ and yellow endosperm$_2$

Since both of these characters are linked with vivipary$_2$, it was to be expected that they would show a linkage with each other. F_2 data on this relationship are given in table 5D, and indicate a linkage between R_{e1} and Y_2 with about 11.3 percent crossing over.

The yellow endosperm referred to above is phenotypically and genotypically different from the pale yellow endosperm which has been shown by EYSTER (1924a) to be linked with vivipary. It is obviously different also from the yellow endosperm described by CORRENS (1901) and more recently by others, as the latter has its locus in chromosome V as indicated by its linkage relations with P_l and other genes known to be located in this chromosome. The yellow endosperm described in this paper for the first time has been named yellow endosperm$_2$ and the gene conditioning its development is designated by the symbol Y_2.

Vivipary$_1$ and vivipary$_2$

The F_1 kernels between vivipary$_1$ and vivipary$_2$ contain embryos which become dormant in the seed stage. F_2 progenies yielded a total of 1492 kernels with dormant and 1034 kernels with viviparous embryos. These frequencies represent a deviation of 71 ± 16.8 kernels from the 9:7 ratio which was expected. These results indicate that vivipary$_1$ and vivipary$_2$ are genetically different though phenotypically alike, and that they are inherited independently.

LINKAGE RELATIONS OF VIVIPARY$_3$

Viviparous strains of maize, which are not phenotypically different from those which have already been described in which vivipary is linked with sugary endosperm, have been found recently in my cultures. The observed frequencies are as follows: 1107 kernels with starchy endosperm and dormant embryo, 175 kernels with starchy endosperm and viviparous embryo, 164 kernels with sugary endosperm and dormant embryo, and 274 kernels with sugary endosperm and viviparous embryo. These results are in close agreement with calculated frequencies on the basis of linkage between S_u and V_{p3} with 22 percent crossing over.

MANGELSDORF (1926) states that G_{e1}, one of his genes for premature germination, appears to be linked with sugary endosperm with about 40 percent crossing over. This linkage is, however, only inferred by him. It is possible that V_{p3} and the G_{e1} represent the same gene.

LINKAGE RELATIONS OF VIVIPARY$_4$

Vivipary$_4$ is the expression of a gene which has its locus in chromosome I at approximately 11.8 crossover units from the gene for shrunken endosperm. Unfortunately only a single F_2 progeny concerned with the relationship between vivipary$_4$ and shrunken endosperm are available at the present time. More extensive observations have been made but the data are not available. In the F_2 progeny there were 200 kernels with non-shrunken endosperm and dormant embryo, 22 kernels with non-shrunken endosperm and viviparous embryo, 14 kernels with shrunken endosperm and dormant embryo, and 87 kernels with shrunken endosperm and viviparous embryo. These results are in close agreement with calculated frequencies on the basis of linkage between V_{p4} and S_h with 11.8 percent crossing over.

THE OCCURRENCE AND NATURE OF VIVIPARY IN THE PLANT KINGDOM

The almost universal occurrence of vivipary among the most simple plants leads to the general conclusion that vivipary is a fundamental and primitive characteristic of plants, and that dormancy has been acquired as a result of genetic changes in the course of phylogenetic development. Plants which changed genetically in such ways that vivipary became inhibited by unfavorable growth conditions were able to survive periods which are unfavorable to vegetative growth. As a result of the genetic changes which made possible this adaptive response, plants have been able to invade and occupy terrestial habitats where the conditions are not always optimum, or even favorable, for growth.

The occurrence of vivipary in maize as an inherited character is direct evidence that vivipary and dormancy are controlled by genetic as well as environmental factors. The identification of four different genes for vivipary in maize in this preliminary study is evidence that dormancy has been induced by a large number of genes in the course of phylogenetic development.

Dormancy occurs in all of the great divisions of the plant kingdom, due, no doubt, to the interaction of genetic and environmental factors. It has been acquired in spores which develop into gametophytes, and in various sporophytic structures as (1) the zygote or fertilized egg in many algae and

fungi, (2) the embryo sporophyte as in most spermatophytes, and (3) modified stems as tubers of *Solanum tuberosum* and buds of trees and shrubs.

Vivipary is generally characteristic of both gametophyte and sporophyte of the liverworts. In Pellia and Fegatella, the spores even germinate within the sporangia.

In mosses the spores develop directly into gametophytes and fertilized eggs into sporophytes without the intervention of a period of dormancy. The spores of Dicnemon and Eucalptodon, two related genera of mosses, grow into multicellular plant structures while they are still within the sporangia. These structures are easily visible to the unaided eye, and are flat on one surface and three-pointed on the other. Similar multicellular bodies have been observed in *Cleistostoma ambigua*, *Cryphaea macrospora*, and *Cryphaea grecillinia*.

Germination of the spores within the sporangia of liverworts and mosses makes possible a shortening of the protonemal development outside the capsule. This is an important characteristic in epiphytic species since a multicellular body will lose water less rapidly than a filamentous protonema. It is probable that the germination of the spores while they are within the sporangium is caused by genetic factors, and has been retained as a permanent character in species which are aided thereby in the reproduction of new individuals.

In some species of pteridophytes the spores pass through a dormant period before developing into gametophytes, in others they germinate as soon as they are exposed to favorable conditions outside of the sporangium, while in still others the spores germinate within the sporangia. The development of the gametophytes within the sporangia is especially characteristic of the species which grow in moist situations. The sporophytes of the pteridophytes are normally viviparous, as the fertilized egg grows directly into a mature sporophyte without the intervention of a period of dormancy.

In the spermatophytes, the gametophytes are normally viviparous, as the spores develop directly into gametophytes without passing through a period of dormancy. The sporophytes, on the other hand, enter a period of dormancy while they are in an early embryonic stage in development. Since the spermatophytes are more familiar in their sporophyte stage, we have come to regard dormancy, as it occurs in seeds, as a normal characteristic of the seed plants. The fundamental nature of dormancy doubtless varies widely in the different categories of the spermatophytes, and, although it is determined by genetic factors, it is influenced by such environmental factors as moisture, temperature, and available oxygen.

Widely scattered among both monocotyledonous and dicotyledonous angiosperms occur plants which bear sporophytes which forego the period of dormancy in the embryonic stage of development. Only a few of the more outstanding examples can be mentioned here. According to GOEBEL (1923) this type of vivipary is characteristic of the genera Rhizophora, Bruigera, and Ceriops. The embryos of the species of Rhizophora are extraordinary because of the extreme development of the stock-like hypocotyl which in many plants is a half meter long. After the embryo is well developed, it drops off the parent plant and rapidly gains a foothold in the muddy ground. In other genera, as Avicenna, the embryos grow into seedlings within the maturing ovary and have stiff upwardly-bent hairs which serve to attach the seedlings to the soil.

Among the monocotyledonous angiosperms may be mentioned the aroid, Cryptocoryne. The ovules of this aroid have two integuments and the outer, after fertilization, grows into a body composed of loosely arranged parenchyma cells in which the continued development of the embryo takes place. The embryo finally falls from the parent plant enclosed by the thin outer integument and is prepared to make a rapid growth into the soil (GOEBEL 1897).

The occurrence of vivipary in maize as genetic variations indicates that this phenomenon is not limited to plants which normally grow in wet places, though viviparous plants have survival value only in habitats where the conditions for continued growth prevail.

SUMMARY

1. Vivipary, the continuous development of the sporophyte in maize, is determined by genetic factors and is strongly influenced in its expression by environmental factors.

2. Four genes for vivipary have been identified by their linkage relations. Data are presented which indicate that the locus of V_{p1} is in chromosome II, that of V_{p2} is in chromosome VIII, that of V_{p3} is in chromosome III, and that of V_{p4} is in chromosome I.

3. By varying the environmental conditions of the maturing ears of plants which are homozygous and heterozygous for a single factor pair for vivipary, normal and viviparous phenotypes have been produced in practically all possible numerical relationships. These results warn against the liberal assumption of multiple factors, with and without linkage, to account for unusual numerical ratios.

4. Data are given which indicate the approximate locus of each of the genes for vivipary, and show that the genes for reduced endosperm$_1$, re-

duced endosperm$_2$, scarred endosperm$_1$, and yellow endosperm$_2$ have their loci in chromosome VIII.

5. Vivipary is regarded as a primitive plant character which, by the interaction of genetic factors and unfavorable growth conditions, may be inhibited. This temporary inhibition of growth is called dormancy. The ability to pass through a period of dormancy has enabled plants to utilize habitats where unfavorable growth conditions alternate with favorable conditions and has been important undoubtedly in the successful invasion of plants from aquatic into terrestial habitats.

6. Vivipary occurs in all of the great divisions of the plant kingdom, but naturally persists only among plants which live in moist habitats. Viviparous plants are not adapted for passing through unfavorable growth periods and do not persist, therefore, among plants that are exposed to such conditions, as, for example, maize.

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A CROSS BETWEEN MICE WITH DIFFERENT NUMBERS OF TAILRINGS

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Two strains of mice with different numbers of tailrings, the lower average being 143 and the higher 216, have been obtained by selection from a colony of albino *Mus musculus* (FORTUYN 1928, 1930).

Since inbreeding is supposed to lead to increased uniformity there should be a possibility of finding a difference in the number of tailrings between various inbred strains of mice. An opportunity to investigate this point was given to me during my visit in the Department of Genetics of the CARNEGIE INSTITUTION OF WASHINGTON in Cold Spring Harbor, New York, for which I wish to express my sincere gratitude to the Director, Doctor C. B. DAVENPORT, as well as to Doctor E. C. MACDOWELL whose valuable material I was allowed to use.

Among several strains of *Mus musculus* two were found with widely different numbers of tailrings. One strain, called C 58, was a black mouse which had been inbred for seventeen to twenty-four generations. The other strain, called StoLi, was a pink-eyed dilute brown mouse, inbred for fifteen to twenty-two generations.

In 225 mice of each strain the number of tailrings was counted after death (figure 1). In C 58 the average number of tailrings and its mean error appeared to be 172.02 ± 0.47, with a standard deviation of ± 7.13 and a coefficient of variation of 4.14 ± 0.18. For StoLi these figures were 205.41 $\pm 0.46, \pm 6.98$ and 3.39 ± 0.15 respectively. Although there is a slight overlapping of the two groups (figure 1) there can be no doubt about the two strains having a different number of tailrings.

The fact that Doctor MACDOWELL had crossed the two strains enabled me to study the number of tailrings in the hybrids (see figure 1). Only fifty-seven hybrids whose mother had been C 58, whereas the father had been StoLi, were available for counting. In thirty-four of these mice the number of tailrings was not counted after death, but while the animal was under ether. It is thought that this did not interfere with the accuracy of the counting. The average number of tailrings in these hybrids was 188.38 ± 0.80 with a standard deviation of ± 6.04 and a coefficient of variation of 3.20 ± 0.29. For the reciprocal type of hybrid (mother StoLi and father

C 58) 110 animals were available and the average number of their tailrings was 194.24 ± 0.62 with a standard deviation of ± 6.59 and a coefficient of variation of 3.39 ± 0.22. The hybrids may be called intermediate which is according to expectation[1], but it is interesting to note that the reciprocal hybrids are different, deviating from one another towards the maternal side. The difference between StoLi × C 58 and C 58 × StoLi is 5.86 ± 1.01 tailrings and is therefore significant. It is remarkable that the average number of tailrings of C 58 × StoLi (188.38) differs only by a fraction of a

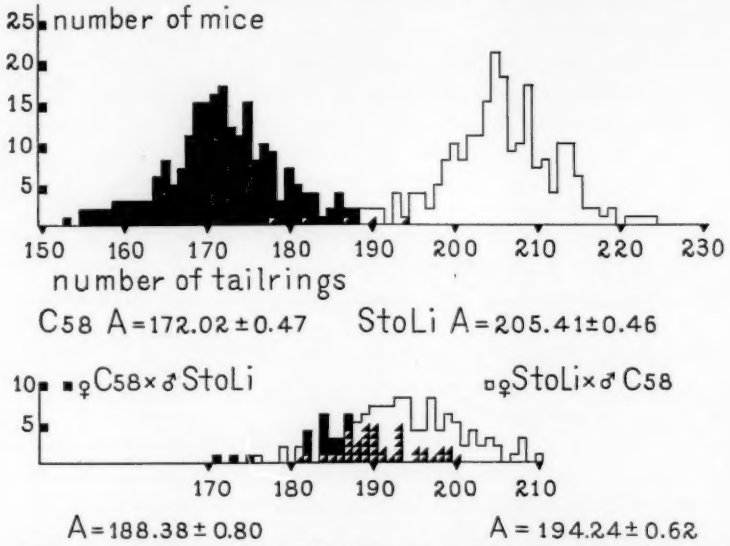

FIGURE 1.—A cross between mice with different numbers of tailrings. The upper part of the figure shows the frequency polygons for the number of tailrings in strain C 58 (solid squares) and in StoLi (outline). A black and a white triangle represents one mouse of each strain with the same number of tailrings. The lower part of the figure shows the same for the reciprocal hybrids C 58 × StoLi (solid) and StoLi × C 58 (outline).

tailring from the arithmetical mean between the two parent races (188.71), whereas the average number of tailrings of StoLi × C 58 (194.24) is almost exactly twice as far from the average of C 58 as from the average of StoLi (194.28).

Besides these hybrids of the F_1 generation two of the eight possible back-

[1] GATES (1926) crossed a black-and-white Japanese waltzer with an average number of tailrings of 141.0 with a pink-eyed dilute brown *Mus musculus* with an average of 180.8 tailrings and obtained a hybrid with an average of 170.0 tailrings.

crosses were made by Doctor MACDOWELL in sufficiently large numbers to allow me to study the number of their tailrings. These two backcrosses were the reciprocal backcrosses between C 58×StoLi and StoLi. In 225 mice the mother was a hybrid (C 58×StoLi) and the father a pure StoLi. The number of their tailrings varied between 172 and 217 with an average of 193.74±0.49, a standard deviation of ±7.47 and a coefficient of variation of 3.85±0.18. In 135 mice in which the mother was StoLi and the father a hybrid (C 58× StoLi) the number of tailrings varied between 180 and 215 with an average of 197.18±0.63, a standard deviation of ±7.41 and a coefficient of variation of 3.75±0.22.

In the first place it may be mentioned that these reciprocal backcrosses again differed in the number of their tailrings. The difference between the two was 3.44±0.79 tailrings and is, therefore, significant. Both backcrosses were intermediate between their parents (StoLi×[C 58×StoLi] being almost exactly halfway), and, like the hybrids, they deviated from one another toward the maternal side.

In (C 58×StoLi)×StoLi the number of tailrings was calculated for each of the two sexes. In 99 males the average number was 193.85±0.70, in 126 females 193.72±0.70. The difference, therefore, was 0.13±0.99 and it may be concluded that the two sexes do not differ in the number of tailrings, a result in agreement with previous work (FORTUYN 1930).

Attention must also be paid to the fact that the coefficients of variation of the backcrosses were not higher than they were in the parent races or in the hybrids. In the parent races these were 4.14±0.18 and 3.39±0.15 and in the backcrosses 3.85±0.18 and 3.75±0.22. This is contrary to expectation. Intermediate hybrids are often intermediate, because the parents differ in many hereditary characters and each contributes a number of dominant characters to its offspring. In such cases the hybrid will be uniform, but the backcrosses will be much more variable than either parent on account of Mendelian segregation. In our particular case this is demonstrated by the color of the mice. Both parent races were uniform in color, one being black and the other pink-eyed dilute brown. The black hybrid in F_1 was also uniform in color. The offspring of this hybrid, however, crossed back to StoLi, the pink-eyed dilute brown parent, showed eight different colors, because black (really: dark-eyed intense black) differs from pink-eyed dilute brown in three genes.

Why the number of tailrings in the backcross was not more variable than it was in the parents remains unexplained. Linkage of characters may have to do with it, but in the backcrosses no difference in the number of tailrings could be found between the different combinations of color fac-

tors. Since the difference between the reciprocal hybrids and backcrosses also requires further investigation, I intend to repeat the experiment with my own mice mentioned in the beginning of this paper.

SUMMARY

Two strains of inbred *Mus musculus* were found to have different numbers of tailrings.

Their hybrids were intermediate, but the two reciprocal hybrids differed, each one deviating to the maternal side.

Two reciprocal backcrosses of this hybrid to one of the parent races also had different numbers of tailrings. In one of them no difference was found between the two sexes.

The coefficients of variation for the number of tailrings were not higher in the backcrosses than they were in the parent races. No indication of Mendelian segregation was found.

No difference was detected between the backcrosses with different combinations of color factors.

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THE ASSOCIATION OF SEMISTERILE–1 IN MAIZE WITH TWO LINKAGE GROUPS[1,2]

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INTRODUCTION

In 1925 there appeared in one of the senior writer's cultures of maize a few plants producing 50 percent aborted pollen. Subsequent examination of the ears borne by these individuals revealed that they likewise developed only one-half the normal number of seeds. Following BELLING'S (1914) application of the term to a similar condition in Stizolobium, the phenomenon was called semisterility. The pedigreed line to which the

[1] Papers from the Department of Genetics, Agricultural Experiment Station, UNIVERSITY OF WISCONSIN, No. 118. Published with the approval of the Director of the Station.

[2] These studies have been carried on, in considerable part, through support from the Research Fund of the UNIVERSITY OF WISCONSIN and a grant-in-aid from the NATIONAL RESEARCH COUNCIL. The authors desire to express their appreciation to the two respective committees for this assistance.

plants belonged was normal in the preceding generation and was not subjected to any treatment calculated to bring about such a change as this. In the sense that the semisterility was not the outcome of any conscious effort to alter the character of the stock it can be said, therefore, to have arisen spontaneously.

The case of partial sterility considered in the present paper is designated as semisterile−1. Subsequent to the discovery of this stock two additional examples of partial sterility were found in our cultures, which BURNHAM (1930) has shown to be distinct. These have been designated as semisterile−2 and semisterile−3, respectively. In the present discussion the term semisterile refers to semisterile−1 except where otherwise indicated.

Breeding tests have shown that semisterile−1 plants when selfed or mated reciprocally with normal individuals produce fully fertile and semisterile offspring in equal numbers (BRINK and BURNHAM 1929). The condition is inherited, therefore, in a very precise manner. At first sight the transmission of semisterility through the gametophyte appears to be an anomalous situation. The condition is manifested by abortion of one-half the pollen grains and embryo sacs and these, of course, are cut off from the line of inheritance. The ability to produce a definite proportion of semisterile offspring, nevertheless, is passed on to the succeeding sporophytic generation. The obvious conclusion is that some of the functional spores carry the complex responsible for semisterility. The breeding facts show that one-half the microspores and macrospores which develop are of this type.

One-half the fertile offspring of self-pollinated semisterile plants are of a new type, called "x-normal" in contradistinction to the original or "o-normal" sort. The x-normal individuals are indistinguishable in appearance from o-normals. When the two classes are crossed, however, all the hybrids are semisterile. Since the occurrence of the x-normal type was demonstrated among the offspring of self-pollinated semisterile plants (BRINK and BURNHAM 1929) the race has been isolated in pure breeding form and its ability to give all semisterile offspring in crosses with ordinary strains of maize confirmed.

In a previous publication (BRINK and BURNHAM 1929) two hypotheses which would account for the origin of semisterility and the breeding facts then at hand were considered. The authors advanced a provisional explanation on the basis of translocation of a part of one chromosome to a non-homologous member of the set. If it is assumed that the modified chromosome pairs assort at random in the reduction divisions and that the spores receiving either the deficient chromosome or the translocated sec-

tion in duplicate abort, the known facts are satisfactorily accounted for. On the other hand, BELLING's (1925) hypothesis of segmental interchange between two non-homologous chromosomes, which has been applied to apparently comparable cases in Stizolobium and Datura, is equally applicable in the present case. According to this interpretation all the aborted spores are deficient for a section of the one or the other of the two chromosomes concerned. Tester stocks of the x-normal type are now being made up with a view of putting these two alternative explanations to a crucial genetic test.

Both the hypotheses mentioned in the preceding paragraph assume a change in one chromosome, which is compensated for in a non-homologous member of the set. In other words, two pairs of chromosomes appear to be involved in the phenomenon. A means of determining genetically the particular chromosomes concerned is afforded by the fact that in semisterile plants linkage should be shown between semisterility and the genes adjacent to the "translocation loci," or points of break or attachment, in the modified groups. Moreover, the amount of linkage should vary according to the position, with reference to the translocation locus, of the gene under test, providing that the type of chromosomal rearrangement responsible for semisterility does not entirely preclude crossing over. In the present paper the results of linkage experiments designed to reveal the two pairs of chromosomes affected and the approximate positions within these of the respective translocation loci are presented. One of the authors (COOPER) has recently undertaken a cytological study of the material and the results of his observations are considered in relation to the breeding data.

OCCURRENCE OF A CHROMOSOME RING IN SEMISTERILE—1

The cytological study was made from aceto-carmine smear preparations of pollen mother cells. Portions of young staminate inflorescences were collected and fixed in a modification of Carnoy's fluid (3 parts 95 percent alcohol, 1 part chloroform and 1 part glacial acetic acid) for periods of 15 to 30 minutes. The material was then washed in 95 percent alcohol for six to twelve hours and stored in 80 percent alcohol. This procedure not only gives excellent aceto-carmine preparations but when mounts are made by the paraffin process, little, if any, shrinkage occurs.

It is a well established fact that 10 bivalent chromosomes are regularly found at diakinesis in the microsporocytes of normal maize plants. This is illustrated in figure 1, B. BURNHAM (1930) has reported that in semisterile—1 individuals only eight bivalents occur, the remaining four chromosomes

forming a group arranged in a ring or very rarely in a chain. We have examined preparations from numerous semisterile−1 plants and find that almost invariably they show this situation. Occasionally a pollen mother

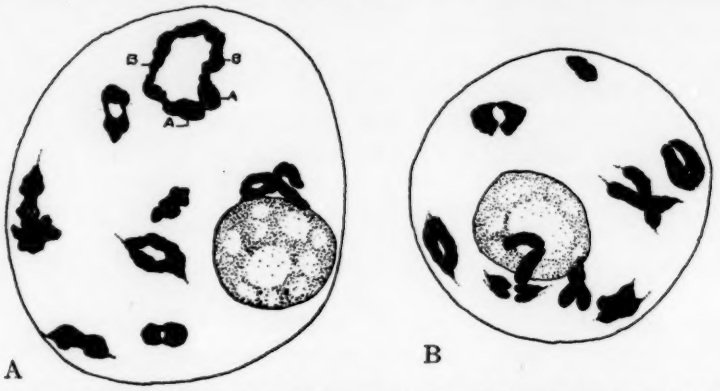

FIGURE 1.—Diakinesis (*Zea Mays*). A. Microspore mother cell of a semisterile-1 plant showing chromosome ring and eight bivalent chromosomes. B. Microspore mother cell of o-normal plant showing ten bivalent chromosomes. ×2900.

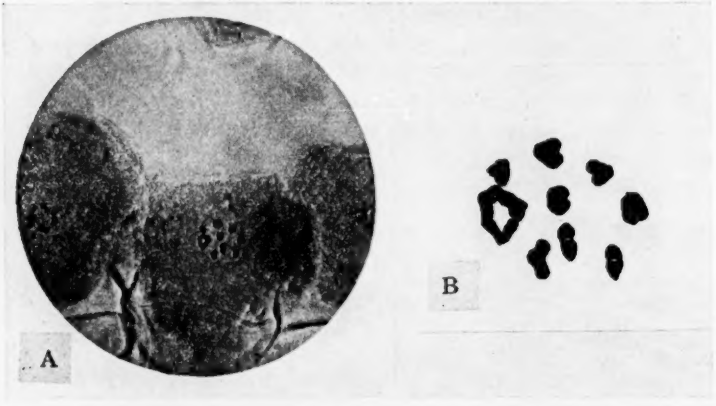

FIGURE 2.—Polar view of heterotypic equatorial plate showing eight bivalents and the chromosome ring. A. Photomicrograph ×750. B. Camera lucida drawing of A. ×1550.

cell is found having 10 bivalent chromosomes. The eight bivalent chromosomes and ring of four as seen at diakinesis are shown in figure 1, A.

On the heterotypic equatorial plate the chromosomes are closely grouped

and it is often difficult to make an accurate count in laterial view. Polar views clearly show eight bivalents and a ring as illustrated in figure 2. Toward the end of this stage the chromosomes are somewhat thinner and can be counted readily.

LINKAGE EXPERIMENTS

Nine linkage groups corresponding, presumably, to nine of the ten chromosomes characteristic of the species, have been recognized in maize. While certain of these groups must still be considered tentative, analysis of the germinal organization of the plant has proceeded to a point where a highly useful body of fact is available for the genetical study of such a condition as semisterility. The mode of attack employed in the present investigation is based upon the chromosome maps of maize now at hand. These maps have been critically revised under date of April 17, 1930, by the Department of Plant Breeding at CORNELL UNIVERSITY and issued to maize geneticists in mimeographed form. In accordance with the senior writer's findings during the past summer, however, that a new dominant gene, Ragged, is rather closely linked with tassel seed−4 and with dwarf−1 and loosely linked with the *a* factor for plant and aleurone color, the two linkage groups presented in the summary as $a-t_{s4}$ and d_1-p_{o2} are considered now as one.

In testing for the possible association of semisterility with a particular chromosome, semisterile plants were out-crossed to stocks carrying known genes in that chromosome and the semisterile hybrids backcrossed to the appropriate normal (that is, not semisterile) recessives. Since the semisterile condition is always manifested when it is present in a plant, this type of mating is equivalent to backcrossing in the coupling phase when, as was usually the case, the partially sterile parent carried the dominant member of the gene pair being used.

In all cases but one, classification for semisterility was made by examination of the pollen. A short branch of the tassel containing mature or nearly mature anthers was collected in the field from each plant during the flowering stage and preserved in a formalin-alcohol solution. In segregating progenies the tassel branches from the different classes of individuals were placed in separate containers. By mounting the anthers on a slide in a dilute iodine solution and macerating them, semisterile plants may be readily distinguished from normal ones by noting under the microscope the proportion of aborted pollen grains. In semisterile individuals, 50 percent of the grains are devoid of starch and hence stain but lightly with iodine whereas the pollen from normal plants assumes a purplish-black color.

Aside from a comparatively few exceptional cases as noted below all the plants in the segregating progenies were thus readily separated into two well defined classes as regards fertility, semisterile and normal.

TABLE 1

The genes used as testers arranged according to linkage groups.

LINKAGE GROUP	NAME OF GENE USED AND SYMBOL	APPROXIMATE LIMITS IN CROSS-OVER UNITS OF MAP DISTANCE EXPLORED
$c-s_h-w_x$	c, aleurone color; s_h, shrunken; w_x, waxy.	95
$r-g_1$	r, aleurone color; g_1 golden.	90
s_u-T_u	s_u, sugary; T_u, tunicate.	100
$b-l_g$,	l_g liguleless; s_i, silkless, v_4, virescent; t_{s1} tassel seed.	110
$V-P_l$	P_l, purple plant color.	70
$P-b_r$	P, pericarp color; t_{s2}, tassel seed; b_r, brachytic; f, fine-striped; a_n, anther ear; a_d, adherent.	120
r_a-g_{l1}	r_a, ramosa; B_n, brown aleurone; i_j, iojap.	120
p_r-v_2	p_r, red aleurone; v_2 virescent; b_v, brevis; b_t, brittle.	110
a_1-t_{s4}	a_1, aleurone and plant color; t_{s4}, tassel seed; R_g, ragged; d_1, dwarf; c_r, crinkly; p_{g2}, pale green.	160
Unplaced genes	b_{m2}, brown midrib; g_2, golden; j, japonica.	

The stocks which were used as testers in these experiments are listed in table 1 according to the respective linkage groups to which they have been assigned. The numerous papers in which the various characters are described and their linkage relations shown are referred to, with a few exceptions, in a recent publication by PHIPPS (1929). It will be unnecessary, therefore, to repeat this information here. Brief mention will be made, however, of two stocks used which have not yet been reported in the literature, brown midrib (b_{m2}) and ragged (R_g).

The brown midrib (b_{m2}) race was isolated at Madison, Wisconsin, from an inbred strain of Golden Glow field corn. Plants of this type, at the half-grown stage, develop brown pigment in the midrib of the leaf and along the veins of the leaf sheath. Unpublished tests by C. R. BURNHAM show that b_{m2} is genetically different from the other brown midrib types which have been reported. The breeding results which have been obtained with b_{m2} in relation to semisterility, as discussed later in this paper, indicate that the gene lies in either the $B-l_g$ group or the $P-b_r$ group. Tests with all the genes known to lie in these chromosomes have not been completed but so far the apparent linkage is not definitely confirmed.

Ragged (R_g) is a monohybrid dominant character which was first observed in a single plant in the corn improvement plot at the WISCONSIN

AGRICULTURAL EXPERIMENT STATION in 1927. Ragged plants are somewhat variable in appearance but all show longitudinal chlorotic areas on the leaves which frequently split asunder. At the flowering stage the foliage of ragged individuals is often considerably torn. Not infrequently it is hanging in shreds. The ragged character shows about 2 percent crossing over with t_{s4}, about 12 percent with d_1 and approximately 42 percent crossing over with a_1 (BRINK and SENN 1931).

Tests with genes in the c-s_h group[3]

Three genes in the c-s_h linkage group, c, s_h, and w_x, were used to determine if semisterility involves a modification of this chromosome. The results with a single progeny segregating for semisterility and the C, c pair are shown in table 18. If c is independent of semisterility 50 percent recombination is the expected result. The observed value is 6.17 percent less than this. Such a deviation is expected in a population of 173 individuals, however, about once in 16 trials purely as a result of chance.

More extensive data are available from tests with the s_h factor as shown in the same table. The net percentage recombination is 46.18 or 3.82 ± 1.11 percent less than that expected if s_h is independent. Six of the seven progenies show less than 50 percent recombination. It might be concluded that semisterility and the s_h gene are in some way associated in inheritance but the grounds for such a view are by no means secure.

Nine backcross progenies comprising a total of 704 plants were classified for semisterility and the waxy (w_x) and nonwaxy (W_x) characters. The data are summarized in table 18. While, on the average, the percentage of recombination is somewhat lower than 50 percent it does not differ significantly from this value. In only one of the nine subgroups did the distribution show a large departure from random assortment. No explanation is at hand for this exceptional case.

In so far, therefore, as the c, s_h and w_x genes serve to represent this linkage group there is no clear evidence that it is involved in semisterility.

Tests with the R-g_1 group

The behavior in inheritance of semisterility was determined in relation to two genes in this group, r and g_1. The evidence presented in table 18 shows that r is very probably independent of semisterility. The same conclusion may be drawn with respect to g_1 on the basis of the data in table 18.

[3] In the interests of economy the numerical results on the distribution of semisterility in relation to the genes in the seven linkage groups where independent behavior was found are presented in summary form only in table 18. On request the authors will be pleased to put the complete tables at the disposal of interested investigators.

These tests provide no indication that the r-g_1 group is in any way affected by semisterility.

Tests with the S_u-T_u group

In this linkage group the distribution of two genes, s_u and T_u about 29 units apart was followed in relation to semisterility. Extensive evidence from 11 segregating progenies comprising 1243 plants shows that the sugary factor is transmitted independently of the semisterile condition. The data are summarized in table 18. Somewhat fewer recombinations occur, on the average, then are expected on this basis but the deviation from 50 percent is not statistically significant.

In table 18 the results are given on the distribution of T_u with respect to semisterility. In each of the six sub-groups a close approximation to 50 percent recombination was found.

Linkage tests with the s_u and T_u genes indicate, therefore, that this group is not concerned in semisterility.

Tests with the B-l_g group

In 1929 backcross data were obtained showing the inheritance of semisterility in relation to two genes in this group, liguleless (l_g) and virescent–4 (v_4). These factors lie about 43 units apart in the chromosome according to the observations of DEMEREC (1924). F_2 counts were secured also in three progenies segregating for silkless (s_k) and semisterility. ANDERSON'S (unpublished) study shows that the locus of the silkless gene is probably between those for liguleless and virescent–4, about 35 units from liguleless.

TABLE 2

Behavior of semisterility with reference to the liguled (L_g) and liguleless (l_g) and green (V_4) and virescent (v_4) pairs of characters. Backcross data.

PROGENY NUMBER	NUMBER OF PLANTS								
	L_gV_4		l_gV_4		L_gv_4		l_gv_4		Total
	Semi-sterile	Normal	Semi-sterile	Normal	Semi-sterile	Normal	Semi-sterile	Normal	
R489	53	5	44	5	5	44	2	29	187
R490	26	5	20	4	0	11	2	18	86
R491	19	6	20	4	2	14	3	11	79
R492	34	8	19	3	5	29	4	18	120
R493	31	1	23	2	2	26	2	29	116
Totals	163	25	126	18	14	124	13	105	588

Five progenies segregating for semisterility and both l_g and v_4 were classified. The data are presented in combined form in table 2, and sepa-

rately for the two respective characters in tables 3 and 4. Additional counts showing the behavior of liguleless with reference to semisterility were obtained in three other families as presented in table 5. Considering the rela-

TABLE 3

Recombination between semisterility and the liguled (L_g) and liguleless (l_g) pair of characters in progenies R489, R490, R491, R492, and R493.

PROGENY NUMBER	SEMISTERILE		NORMAL		TOTAL PLANTS	PERCENTAGE RECOMBINATION	DEVIATION FROM 50 PERCENT
	L_g	l_g	L_g	l_g			
R489	58	46	49	34	187	50.80	0.80±2.47
R490	26	22	16	22	86	44.19	−5.81±3.65
R491	21	23	20	15	79	54.43	4.43±3.79
R492	39	23	37	21	120	50.00	0.00±3.08
R493	33	25	27	31	116	44.83	−5.17±3.13
Totals	177	139	149	123	588	48.13	−1.87±1.39

TABLE 4

Recombination between semisterility and the green (V_4) and virescent (v_4) genes. Matings of the type (semisterile, green×normal, virescent, F_1)×normal, virescent.

PROGENY NUMBER	SEMISTERILE		NORMAL		TOTAL PLANTS	PERCENTAGE RECOMBINATION	DEVIATION FROM 50 PERCENT
	V_4	v_4	V_4	v_4			
R489	97	7	10	73	187	9.09	−40.91±2.45
R490	46	2	9	29	86	12.79	−37.21±3.64
R491	39	5	10	25	79	18.99	−31.01±3.79
R492	53	9	11	47	120	16.67	−33.33±3.08
R493	54	4	3	55	116	6.03	−43.97±3.13
Totals	289	27	43	229	588	11.90	−38.10±1.39

TABLE 5

Additional data on the relation of liguleless to semisterility.

PROGENY NUMBER	SEMISTERILE		NORMAL		TOTAL PLANTS	PERCENTAGE RECOMBINATION
	L_g	l_g	L_g	l_g		
R516*	57	38	48	26	169	50.89±2.59
R518†	59	38	33	44	174	40.80±2.56
R519‡	41	37	13	22	113	44.25±3.17
Totals	157	113	94	92	456	45.39±1.58

* 1 plant about 90 percent sterile.

† 3 plants completely sterile, 3 plants about 75 percent sterile.

‡ 1 plant completely sterile.

tionship of liguleless first, it is apparent that this character recombines with semisterility in a proportion only slightly less than that expected in cases of independent inheritance. The net percentage of recombination in the seven families studied is 47.41 ± 0.90.

The results with v_4, on the other hand, reveal a very different situation. The average percentage recombination in this case is 11.90. This is a deviation of 38.10 ± 1.30 percent from the value expected if v_4 is inherited independently of semisterility. It is clearly apparent that the V_4, v_4 pair and the complex governing semisterility tend to assort together. Since l_g, in the same progenies, shows about 47 percent recombination with semisterility it may be concluded that the change in the B-l_g group responsible for the partial sterility involves only a portion of the chromosome and that the affected portion lies in the vicinity of the v_4 locus.

On the basis of the results in table 2, l_g and v_4 show 47.96 percent recombination, l_g and semisterility, 48.13 percent, and v_4 and semisterility, 11.90 percent. These values may be interpreted to mean that the chromosome part involved in semisterility (considering the portion bearing l_g as basal) lies on the side of v_4 remote from the liguleless gene.

The F_2 results obtained with silkless (s_k) are in accord with this conclusion. The silkless character and semisterility show a net recombination value of 24.21 percent (table 6) as computed by the coefficient of association

TABLE 6

Recombination between semisterility and the non-silkless (S_k) and silkless (s_k) genes. Progenies are from (semisterile, $S_k \times$ normal, s_k) plants selfed.

PROGENY NUMBER	SEMISTERILE		NORMAL		TOTAL PLANTS	PERCENTAGE RECOMBINATION
	S_k	S_k	S_k	S_k		
R592	36	13	53	17	119	23.31
R593	57	10	51	6	124	19.67
R594	30	13	20	10	73	27.10
Totals	123	36	124	33	316	24.21

method (COLLINS 1924). Backcross data on the behavior of s_k were obtained in 1930. Through an oversight, pollen from the segregating progenies was not collected, but the omission was discovered in time to classify the S_k plants for semisterility on the basis of the number of seeds formed on the ears. The results as presented in table 7 show about 35 percent recombination, on the average, between silkless and semisterility. The departure from the 50 percent expected on random assortment is clearly significant statistically.

TABLE 7

Backcross data from the cross (semisterile, non-silkless×normal, silkless)×normal, silkless. Only the non-silkless plants were classified for semisterility.

PROGENY NUMBER	NON-SILKLESS		PERCENTAGE RECOMBINATION	DEVIATION FROM 1:1 RATIO IN NUMBERS
	Semisterile	Normal		
R681	27	19	41.30	4±2.29
R682, a	72	34	32.07	19±3.47
Totals	99	53	34.88	23±4.16

The distribution of tassel seed–1 (t_{s1}) with reference to semisterility is shown in table 8. The T_{s1} plants were classified for semisterility according to the character of the pollen produced. This could not be done for the re-

TABLE 8

Recombination between semisterility and the non-tassel seed (T_{s1}) and tassel seed (t_{s1}) characters. Data from matings of the type normal, tassel seed×(normal, tassel seed×x-normal, non-tassel seed, F_1).

PROGENY NUMBER	NON-TASSEL SEED-1		PERCENTAGE RECOMBINATION	DEVIATION FROM 1:1 RATIO IN NUMBERS
	Semisterile	Normal		
R711	99	13	11.61	43±3.57

cessive t_{s1} plants, however, since they form only pistillate flowers. The ears on the t_{s1} plants were bagged and held for a few days during the flowering season in order to pollinate them with a certain later maturing stock. The delay resulted in so many poorly filled ears that an accurate count of the semisteriles and normals could not be made. Table 8, consequently, is based on the non-tassel seed individuals only. Approximately 12 percent recombination is shown between t_{s1} and semisterility in the population of 112 plants.

Tests with the Y-P_l group

The behavior of semisterility was studied with reference to only one pair of genes in this group, P_l, p_l, which, in combination with A_1 and B, differentiate between purple and sun red plants (EMERSON 1921). The one backcross family obtained, comprising 224 individuals, shows exactly 50 percent recombination between the characters concerned (table 18).

Tests with the P-b_r group

As shown in table 9 semisterility appears to be inherited independently of colored pericarp (P). Counts were made in six progenies from back-

TABLE 9

Recombination between semisterility and the colored pericarp (P) and colorless pericarp (p) genes. Matings of the type (semisterile, colorless pericarp×normal, colored pericarp, F_1) ×normal, colorless pericarp.

PROGENY NUMBER	SEMISTERILE		NORMAL		TOTAL PLANTS	PERCENTAGE RECOMBINATION	DEVIATION FROM 50 PERCENT
	P	*p*	*P*	*p*			
R348, a	27	25	27	27	106	50.97	0.97±3.28
R349, a	17	17	9	7	50	48.00	−2.00±4.77
R350, a and b	9	7	6	5	27	51.85	1.85±6.49
R351, a	13	32	19	18	82	37.81	−12.19±3.72
R352, a	49	35	42	46	172	55.23	5.23±2.57
R353, a, b and c	20	4	9	8	41	68.29	18.29±5.27
Totals	135	120	112	111	478	51.47	1.47±1.54

crosses and in only one of these, R353, a, b and c, is there a large deviation from 50 percent recombination. The net percentage of recombination based on 478 plants is 51.47 percent.

The tassel seed character (t_{s2}), which is closely linked with *P* (EMERSON 1920), is likewise independent of semisterility. Homozygous t_{s2} plants do not produce pollen so that only the dominant individuals in the progeny studied were classified for semisterility. As shown in table 10 exactly one-half of the non-tassel seed segregates were semisterile, indicating random recombination.

TABLE 10

Recombination between semisterility and non-tassel seed (T_{s2}) and tassel seed (t_{s2}). Mating of the type (semisterile non-tassel seed×normal, tassel seed)×normal, tassel seed.

PROGENY NUMBER	SEMISTERILE		NORMAL		DEVIATION FROM 1:1 RATIO IN NUMBERS
	T_{s2}	t_{s2}*	T_{s2}	t_{s2}	
R373	99	..	99	..	0.0±4.75

* Not classified for semisterility.

The behavior of semisterility with reference to the brachytic (b_r) and fine-striped (*f*) characters was observed in a distinct group of progenies. Brachytic and fine-striped according to the unpublished studies of EMERSON and of BRUNSON are about five units apart. According to the observations of the same authors, brachytic is approximately 45 units from *P*. BRUNSON (unpublished) has shown that the order is *P*-b_r-*f*. Table 12, which is based on table 11, shows the relation between b_r and semisterility. It will be noted that only 10.12 percent recombination occurs between the two characters in a total population of 682 individuals.

TABLE 11

Behavior of semisterility with reference to the tall (B_r) and brachytic (b_r) and the green (F) and fine-striped (f) pairs of characters. Data from backcrosses of semisterile $B_rF \cdot b_rf$ plants to normal, b_rf.

PROGENY NUMBER	NUMBER OF PLANTS								TOTAL
	B_rF		b_rF		B_rf		b_rf		
	Semi-sterile	Normal	Semi-sterile	Normal	Semi-sterile	Normal	Semi-sterile	Normal	
R530	77	3	1	5	1	1	3	55	146
R531	43	1	1	0	0	0	4	42	91
R532	46	5	4	0	0	2	3	52	112
R703	68	3	4	1	0	2	6	45	129
R704	55	4	4	0	0	1	6	49	119
R705	44	3	3	0	0	2	3	30	85
Totals	333	19	17	6	1	8	25	273	682

TABLE 12

Recombination between semisterility and the tall (B_r) and brachytic (b_r) characters in progenies R530, R531, R532, R703, R704, and R705.

PROGENY NUMBER	SEMISTERILE		NORMAL		TOTAL PLANTS	PERCENTAGE RECOMBINATION	DEVIATION FROM 50 PERCENT
	B_r	b_r	B_r	b_r			
R530	78	4	4	60	146	5.48	-44.52 ± 2.79
R531	43	5	1	42	91	6.59	-43.41 ± 3.54
R532	46	7	7	52	112	12.50	-37.50 ± 3.19
R703	68	10	5	46	129	11.63	-38.37 ± 2.97
R704	55	10	5	49	119	12.60	-37.40 ± 3.09
R705	44	6	5	30	85	12.94	-37.06 ± 3.66
Totals	334	42	27	279	682	10.12	-39.88 ± 1.29

TABLE 13

Recombination between semisterility and the green (F) and fine-striped (f) characters in progenies R530, R531, R532, R703, R704 and R705.

PROGENY NUMBER	SEMISTERILE		NORMAL		TOTAL PLANTS	PERCENTAGE RECOMBINATION	DEVIATION FROM 50 PERCENT
	F	f	F	f			
R530	78	4	8	56	146	8.22	-41.78 ± 2.79
R531	44	4	1	42	91	5.49	-44.51 ± 3.54
R532	50	3	5	54	112	7.14	-42.86 ± 3.19
R703	72	6	4	47	129	7.75	-42.25 ± 2.97
R704	59	6	4	50	119	8.40	-41.60 ± 3.09
R705	47	3	3	32	85	7.06	-42.94 ± 3.66
Totals	350	26	25	281	682	7.48	-42.52 ± 1.29

The amount of recombination between fine striped (*f*) and semisterility is 7.48 percent (table 13). Further evidence on this relation is given in table 14. Four additional progenies comprising 646 plants show 8.67 per-

TABLE 14

Additional data on the relationship of semisterility to the fine-striped (f) character. Matings of the type (semisterile, green×normal, fine-striped)×normal, fine-striped.

PROGENY NUMBER	SEMISTERILE		NORMAL		TOTAL PLANTS	PERCENTAGE RECOMBINATION	DEVIATION FROM 50 PERCENT
	F	*f*	*F*	*f*			
R533	78	11	6	78	173	9.83	−40.17±2.56
R534	79	4	11	62	156	9.62	−40.38±2.70
R535	85	6	10	74	175	9.14	−40.86±2.55
R536*	71	4	4	63	142	5.63	−44.37±2.83
Totals	313	25	31	277	646	8.67	−41.33±1.33

* Progeny segregating tassel seed (t_{s2}?). Tassel seed plants were not classified for semisterility

cent recombination between fine-striped and semisterility. The data point unmistakably to the conclusion that the B_r, b_r and F, f genes tend to assort with the semisterile complex. It appears, therefore, that the partial sterility involves an alteration of the P-b_r chromosome in the vicinity of the b_r and f loci.

The data in table 11 indicate that the change in the chromosome has occurred at a point not far from the f locus on the side remote from b_r. Brachytic and fine-striped show 4.69 percent recombination in these stocks, brachytic and semisterility give 10.12 percent and fine-striped and semisterility, 7.48 percent. From these values the probable order would appear to be brachytic—fine-striped—translocation locus.

The behavior of semisterility in relation to two other genes in the P-b_r group, adherent (a_d) and anther ear (a_n), has been determined. KEMPTON (1922) reports that a_d gives about 25 percent crossing over with b_r and EMERSON and also COLLINS and KEMPTON have unpublished evidence showing that a_n is linked with b_r. The position of these two genes with reference to the others studied in the P-b_r group is not yet known.

The backcross results in table 15 show that anther ear is closely associated with semisterility in inheritance. The average amount of recombination in seven progenies comprising 482 plants is 2.90 percent.

Adherent is even more closely linked with semisterility. As shown in table 16, the net amount of recombination in a population of 497 plants in five backcross progenies is 1.41 percent. In two of the five progenies no recombination occurred.

TABLE 15

Recombination between semisterility and the tall (A_n) and anther ear (a_n) characters. Data from matings of the type (semisterile, tall×normal, anther ear)×normal, anther ear.

PROGENY NUMBER	SEMISTERILE		NORMAL		TOTAL PLANTS	PERCENTAGE RECOMBINATION	DEVIATION FROM 50 PERCENT
	A_n	a_n	A_n	a_n			
R686	43	2	0	53	98	2.04	−47.96±3.41
R687	60	2	0	53	115	1.74	−48.26±3.14
R688	35	0	1	28	64	1.56	−48.44±4.22
R689	13	0	2	12	27	7.59	−42.41±6.49
R690	27	0	2	11	40	5.00	−45.00±5.33
R690.1	37	0	4	29	70	5.71	−44.29±4.03
L425	34	1	0	33	68	1.47	−48.53±4.09
Totals	249	5	9	219	482	2.90	−47.10±1.54

TABLE 16

Recombination between semisterility and the non-adherent (A_d) and adherent (a_d) characters. Data from matings of the type (semisterile, non-adherent×normal, adherent, F_1) ×normal, adherent.

PROGENY NUMBER	SEMISTERILE		NORMAL		TOTAL PLANTS	PERCENTAGE RECOMBINATION	DEVIATION FROM 50 PERCENT
	A_d	a_d	A_d	a_d			
R692	50	2	2	26	80	5.00	−45.00±3.77
R693	60	0	1	57	118	0.85	−49.15±3.10
R694	58	0	0	46	104	0.00	−50.00±3.31
R695	58	0	0	81	139	0.00	−50.00±2.86
R696	33	0	2	21	56	3.57	−46.43±4.51
Totals	259	2	5	231	497	1.41	−48.59±1.51

Since the relations of a_d and a_n to b_r and f in the normal plant have not yet been determined it can not be decided now where the two genes in question lie with reference to the translocation locus. It is quite possible, of course, that they are not as close as the recombination values indicate since the structural change assumed to be responsible for the semisterility may interfere with crossing over near the translocation loci. The evidence obtained on the distribution of the P, t_{s2}, b_r, f, a_d and a_n genes, among the offspring of semisterile plants, however, shows conclusively that this linkage group is one of those concerned in semisterility and that the translocation locus is in the region of the f, a_d and a_n genes.

Tests with the R_a-g_{11} group

Semisterility was tested with four genes in the r_a-g_{11} group, brown aleurone (B_n), glossy (g_{11}), ramosa (r_a) and iojap (i_j). These genes are distrib-

uted over a range of roughly 50 units on the chromosome map (KVAKAN 1924, JENKINS and POPE unpublished). The experiments, therefore, provide a thorough test of this region of the r_a-g_{11} chromosome.

The data presented in table 18 show that semisterility segregates independently of the B_n, b_n pair of genes. The same conclusion may be drawn with reference to g_{11} on the basis of the results in table 18. Two progenies segregating for ramosa and semisterility gave, on the average, 50.36 percent recombination. The summarized results are shown in table 18. According to the data presented in table 18, iojap, likewise, assorts independently of semisterility.

All the genes tested in the r_a-g_{11} group, therefore, recombine at random with the semisterile complex.

Tests with the P_r-v_2 group

PHIPPS (1929) has shown that the genes differentiating purple and red aleurone (P_r, p_r) and a virescent (v_2) probably reside in the same linkage group. In a population of 1774 individuals, 41.9 percent crossing over was observed. BURNHAM (unpublished) has obtained evidence that brittle (b_t) is linked with p_r and LI (unpublished) finds that brevis (b_v) likewise falls in the p_r-v_2 group. Semisterility has been tested with these four characters.

The summarized data relating to p_r are presented in table 18. The average percentage recombination is 49.77, a value which shows that p_r and semisterility are inherited independently.

As shown in table 18, v_2 and semisterility likewise behave independently. In a total population of 1025 plants the amount of recombination is 49.66 percent.

The results obtained in the test with brittle are given in summary form in table 18. Only the non-brittle seeds from the segregating ears were planted and these gave equal numbers of normal and semisterile plants within the limits of random sampling.

The results obtained in two of the backcross progenies segregating for the dwarf, brevis, and semisterility indicated random assortment. Two other progenies gave significantly more than 50 percent recombination. The cause of this irregular behavior is unknown. The result, however, is not one which would be expected if b_v and semisterile-1 were associated in inheritance. In the total population there is 57.89 percent recombination (table 18).

So far, therefore, as tests with the p_r, v_2, b_t and b_v genes serve to reveal the situation, the p_r-v_2 group behaves independently of semisterility.

Tests with the A_1-t_{s4} group

The behavior of semisterility has been determined in relation to seven genes in the a_1-t_{s4} group, a_1, t_{s4}, n_a, R_g, d_1, c_r and p_{g2}.

The data in table 18 show that semisterility assorts independently of the A_1, a_1 pair. In a total population of 724 plants, 48.34 percent of the individuals fall in the recombination classes.

The distribution of t_{s4} with reference to semisterility is also shown in table 18. The average percentage recombination is 47.81, indicating that the two characters are probably inherited independently.

The results obtained with n_a are presented in condensed form in table 18. In all three progenies tested there was a deficiency of recessive plants. This was particularly marked in R547 where the ratio of talls to dwarfs was approximately 5:1. Was the pistillate parent of this progeny trisomic for the a_1-t_{s4} chromosome? Such a distribution might well result from a $N_a\ N_a\ n_a \times n_a\ n_a$ combination. In spite of these irregularities in the n_a ratio, however, it is reasonably clear that semisterility and the dwarf are inherited independently.

As shown in table 18 the dwarf, d_1, and semisterility recombine at random.

The results with crinkly (c_r) are rather irregular. In each of the four progenies upon which the entry in table 18 is based there was a rather well marked deficiency of c_r plants and in one of the progenies 12 plants were entirely sterile. The deficiency in the number of crinkly individuals may be due in part to incorrect classification since C_r and c_r plants are not easily distinguished in some progenies. It appears probable that the apparently significant deviation from 50 percent recombination is due to some extraneous factor of this sort rather than to an effect of semisterility on the distribution of the C_r, c_r genes.

As seen in table 18, pale green (p_{g2}) and semisterility are transmitted independently.

One progeny segregating for the dominant character ragged, R_g, and semisterility was studied. Eighteen plants were almost if not completely sterile, eight others showed about 75 percent pollen abortion and the proportion of ragged individuals is considerably lower than is usually the case in $R_g r_g \times r_g r_g$ backcrosses. The amount of recombination, however, between R_g and semisterility, is 50.26 percent, indicating random assortment (table 18).

It may be concluded from these facts that semisterility is inherited independently of the genes in the a_1-t_{s4} linkage group.

Tests with genes whose linkage relations are unknown

Golden (g_2)[4]

Five progenies from backcrosses of semisterile plants heterozygous for g_2 (JENKINS 1926) to normal, g_2 plants were grown. The summarized results given in table 18 showing 53.02 percent recombination indicate that independent inheritance probably prevails.

Brown midrib (b_{m2})

The b_{m2} gene, which is distinct from the one studied by EYSTER (b_{m1}), has not yet been assigned to a linkage group. Its behavior in relation to semisterility is shown in table 17. In five of the six progenies the amount of

TABLE 17

Recombination between semisterility and the green midrib (B_{m2}) and brown midrib (b_{m2}) genes. Matings of the type (semisterile, green midrib×normal, brown midrib, F_1)×normal, brown midrib.

PROGENY NUMBER	SEMISTERILE		NORMAL		TOTAL PLANTS	PERCENTAGE RECOMBINATION	DEVIATION FROM 50 PERCENT
	B_{m2}	b_{m2}	B_{m2}	b_{m2}			
R338, a and b	75	39	40	56	210	37.62	−12.38±2.33
R595*	73	34	45	65	217	36.40	−13.60±2.29
R596†	71	61	60	57	249	48.43	−1.57±2.14
R597‡	112	68	87	114	381	40.68	−9.32±1.73
R598§	108	73	86	119	386	41.19	−8.81±1.72
R599	76	33	53	59	221	38.91	−11.09±2.27
Totals	515	308	371	470	1664	40.80	−9.30±0.84

* Six plants almost or completely sterile, 1 plant showing about 75 percent pollen abortion.
† Five plants almost or completely sterile, 3 plants showing about 75 percent pollen abortion.
‡ Twelve plants almost or completely sterile.
§ One plant possibly completely sterile, 1 plant showing about 75 percent pollen abortion.

recombination between b_{m2} and semisterility appears to be significantly less than 50 percent. The actual values range from 36.40 percent to 41.19 percent. The remaining progeny, R596, shows 48.43 percent recombination. When the total population is considered the recombination value is 40.80 percent, an amount 9.30 ± 0.84 percent less than that expected if b_{m2} and semisterility assort independently. These results strongly suggest that b_{m2} is carried by one of the chromosomes concerned in semisterility. This would mean that its locus is in either the *B-l*$_g$ chromosome or the *P-b*$_r$ chromosome.

[4] The cream character found by Doctor C. M. WOODWORTH, UNIVERSITY OF ILLINOIS, is identical with golden-2.

Japonica (*j*)

The summarized results on the behavior of japonica with reference to semisterility are given in table 18. In each of the nine progenies the percentage recombination does not deviate from 50 percent by an amount greater than might frequently arise from chance. Japonica, therefore, is very probably independent of semisterility.

TABLE 18

Summary of results on the distribution of semisterility in relation to genes in seven linkage groups which assort at random with the semisterile complex. Backcross data.

GENES TESTED		SEMISTERILE		NORMAL		TOTAL PLANTS	NUMBER OF PROGENIES	PERCENTAGE RECOMBINATION	DEVIATION FROM 50 PERCENT
X	x	X	x	X	x				
						C-s_h-w_x group			
C	*c*	36	42	34	61	173	1	43.93	−6.17±2.56
S_h	s_h	247	229	200	253	929	7	46.18	−3.82±1.11
W_x	w_x	197	162	168	177	704	9	46.87	−3.12±1.27
						R-g_1 group			
R	*r*	215	207	215	207	844	6	50.00	0.00±1.16
G_1	g_1	319	289	249	277	1134	8	47.44	−2.56±1.01
						S_u-T_u group			
S_u	s_u	335	289	307	312	1243	11	47.95	−2.05±0.97
T_u	t_u	179	146	178	134	637	6	49.14	−0.86±1.34
						Y-P_l group			
P_l	p_l	46	65	47	66	224	1	50.00	0.00±2.25
						R_a-g_{11} group			
B_n	b_n	156	179	159	163	657	3	48.55	−1.45±1.32
G_{11}	g_{11}	216	210	183	140	749	5	52.47	2.47±1.23
R_a	r_a	61	69	70	76	276	2	50.36	0.36±2.03
I_j	i_j	250	125	216	106	697	5	48.92	−1.08±1.28
						P_r-v_2 group			
P_r	p_r	188	134	192	141	655	8	49.77	−0.23±1.32
V_2	v_2	326	220	289	190	1025	5	49.66	−0.34±1.06
B_t	b_t	179	..	159	..	338	5	47.04	−2.96±1.83
B_v	b_v	70	51	92	34	247	4	57.89	7.89±2.15
						A_1-l_{s4} group			
A_1	a_1	200	171	179	174	724	4	48.34	−1.66±1.25
T_{s4}	t_{s4}	132	102	95	83	412	2	47.81	−2.19±1.66
N_a	n_a	85	52	94	23	254	3	57.48	7.48±2.12
D_1	d_1	291	185	289	157	922	7	51.41	1.41±1.11
C_r	c_r	209	177	232	138	756	4	54.10	4.10±1.23
P_{g2}	p_{g2}	304	128	237	90	759	6	48.09	−1.91±1.22
R_g	r_g	77	131	61	117	386	1	50.26	0.26±1.72
						Unplaced genes			
G_2	g_2	288	337	243	226	1094	5	53.02	3.02±1.07
J	*j*	371	321	289	313	1294	9	47.14	−2.86±0.97

Plants with irregular proportions of aborted pollen were found in certain groups as follows *R*, 4; s_u, 8; T_u, 11; P_l, 8; B_n, 7; g_{11}, 38; i_j, 5; v_2, 5; b_t, 1; a_1, 12; l_{s4}, 26; n_a, 30; d_1, 12; c_r, 21; p_{g2}, 17; R_g, 26; g_2, 15; *j*, 13.

THE PROPORTION OF ABORTED POLLEN GRAINS IN SEMISTERILE-1 PLANTS

In an earlier publication (BRINK 1927) data were presented showing that approximately 50 percent of the pollen in semisterile-1 plants aborted. The actual proportion of defective grains observed was 51.6 percent, based on counts from four plants. An accurate determination of this value is important since the amount of sterility is dependent upon the manner in which the modified and the normal chromosomes in the two affected sets assort in the reduction divisions.

In order to establish the amount of pollen abortion on a broader basis the number of defective grains was counted in 198 semisterile plants from three segregating sib progenies, R489, R490 and R492. A small piece of an anther from each plant was macerated in a mixture of glycerol and water containing 0.3 percent of iodine. With this treatment the normal pollen grains, which are rich in starch, stain deeply, whereas the aborted grains remain almost unchanged in color. The size of the piece of anther taken was so regulated that all the pollen grains within it could be counted readily under a binocular microscope equipped with crosshairs. In this way the difficulties arising in sampling due to the tendency of the aborted grains to float towards the periphery of the drop when mounted on a slide were overcome. Roughly 300 pollen grains from each individual were counted, a number which is quite adequate to give a dependable value.

The results obtained are presented in the form of a frequency distribution in table 19 and graphically in figure 3.

TABLE 19

Frequency distribution of percentage of aborted pollen in three sib progenies, R489, R490, and R492.

PERCENT ABORTED POLLEN	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	TOTAL
Frequency	1	2	0	0	2	3	7	11	19	20	27	15	22	23	19	9	4	3	5	2	1	0	0	0	1	1	0	1	1	199

The mean percentage of aborted pollen grains for the 198 plants is 50.25. The deviation from equality of normal and aborted grains, 0.25 ± 0.190 percent, is well within the limits of random sampling. It may be concluded, therefore, that, on the average, almost exactly one-half the pollen grains produced by semisterile-1 plants are aborted and one-half are normal.

A further point in this connection remains to be considered. Are the percentages of aborted pollen for the individual plants distributed around the mean value in the form of a normal curve? In other words, are the devia-

tions from 50 percent such as would be expected if chance alone is operating?

This question may be answered, in a general way, by comparing the actual distribution in figure 3 with the normal frequency curve which has been fitted to it. It may be seen that the two curves are in fairly close agreement with each other. It would appear doubtful, however, whether the position of the few variates at the extremes of the observed distribu-

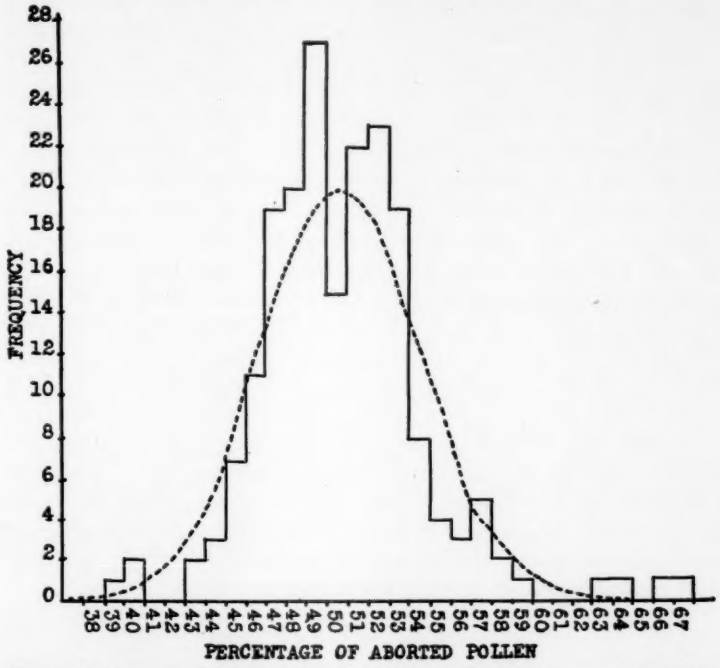

FIGURE 3.—Frequency distribution of semisterile plants with respect to percentage of aborted pollen in three sib progenies. The broken line shows a normal curve of the same area and standard deviation.

tion is the result of pure chance. Quite probably these variates are fluctuating around norms other than 50 percent.

A more exact means of evaluating the observed variation is afforded by a method which YULE (1914) has proposed.[5] The actual standard devia-

[5] If p is the probability of obtaining one of the two allelomorphic characters and q the chance of obtaining the other, the expected standard deviation of the proportion in a group of samples of different sizes is equal to $\sqrt{pqr}$, where r is equal to the reciprocal of the harmonic mean of the numbers in the samples.

tion is compared with that expected if the distribution is strictly normal. The observed standard deviation is 3.97 ± 0.130 percent. The expected value, computed by YULE's formula, is 3.03 ± 0.103 percent. The difference between the observed and calculated values, 0.94 ± 0.166 percent, is over 5.5 times its probable error and would be expected as a result of chance alone only once in many thousand trials.

It is quite certain, therefore, that while the mean percentage of aborted pollen grains is almost exactly 50 percent the variations from this value are somewhat larger than can reasonably be ascribed to chance alone.

Two factors may be suggested as possibly involved in causing statistically significant departures from 50 percent in the proportion of aborted pollen grains. On the hypothesis that the abortion is due to deficiency, any plant which carries an extra normal member of the two chromosome pairs involved in semisterility will produce less than 50 percent aborted grains, the extra chromosome making good the deficiency in a certain proportion of the cases. Amounts of sterility greater than 50 percent are more difficult to account for. If the possibility of changes within additional non-homologous chromosomes is left aside, one must assume that the assortment of the normal and modified chromosomes in the two affected pairs is not a random one. As to why this should occur in some plants when it evidently does not occur in most of the cases is not apparent.

While no matings have been made to test the possibility, it seems rather likely that many of the plants producing no functional pollen found from time to time in the progenies segregating for semisterility owe their condition to genes of the type which SINGLETON and JONES (1930) have termed "male sterile." Male steriles produce few or no functional pollen grains and the anthers fail to dehisce. In the case which SINGLETON and JONES have studied the condition is due to a simple recessive gene.

There has been no opportunity thus far in the work to examine further those plants referred to in footnotes to the tables as "about 75 percent sterile." With few exceptions the occurrence of these aberrant individuals became known only during post-seasonal examination of the tassels collected from them. Quite possibly some of them involve structural changes in chromosomes other than the two non-homologous pairs concerned in semisterile-1.

THE PROPORTION OF THE TWO CLASSES OF FUNCTIONAL GAMETES PRODUCED BY SEMISTERILE PLANTS

It has been shown above that, within the limits of random sampling, one-half the microspores produced by semisterile plants abort. Presum-

ably the same situation obtains with reference to the embryo sacs. Among the functional spores, that is, those capable of developing into gametophytes, two classes are expected. In the one the chromosomes are normal in their composition while in the second the rearrangement, segmental interchange or translocation, responsible for the partial sterility of the parent plant obtains. A gamete from the first type in combination with a normal gamete will produce an o-normal plant; a gamete of the second type when fertilized by an o-normal gamete will give a semisterile individual. In what proportion do the two types of functional spores occur?

This point may be tested by examining the proportion of semisterile and normal plants occurring in progenies from matings between semisterile and normal plants. All the segregating families which have been used in the present study which contained at least 50 plants have been classified in table 20 according to the percentage of semisterile individuals they con-

TABLE 20

Frequency distribution of percentage of semisterile plants in progenies resulting from semisterile×normal matings.

PERCENT OF SEMI-STERILE PLANTS	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	78	TOTAL
Frequency	1	0	1	0	1	0	2	2	2	5	5	7	8	8	5	5	4	11	4	3	3	7	3	3	1	3	0	0	0	0	0	2	1	97

tained. While the minimum sized progeny used was 50, four-fifths of the families contained over 100 plants and nearly one-half over 150. There are 97 progenies in all available for examination. Of these, 94 are from matings in which the pistillate parent was semisterile. The results, therefore, bear largely on the constitution of the female gametes.

The mean percentage of semisterile plants in the 97 families is 52.35. The deviation from 50 percent, 2.35 ± 3.32 percent, is not larger than would be expected to result frequently from chance. It may be concluded, therefore, that, within the limits of random sampling, one-half the functional spores produced by semisterile plants, on the average, carry the sterility-producing complex. In figure 4, the distribution in table 20 is shown graphically in comparison with a normal curve of the same area. The use of a class interval of one percent gives a frequency polygon of considerable irregularity. With due regard, however, to the effect of the rather fine grouping of the variates it is evident that the "spread" is appreciably greater than that in a population of the same size normally distributed. In other words, it appears that in certain families at least, some factors other

than chance affect the proportion of normal and semisterile individuals. It is evident from the character of the distribution that the proportion of partially sterile plants is increased in some cases and decreased in others.

Regarding the probable nature of the agencies tending to increase the dispersion nothing can now be said. The frequency distribution includes a number of groups of closely related families. There does not appear to be any tendency, however, for certain groups to show a high proportion of semisterile individuals and others a low proportion.

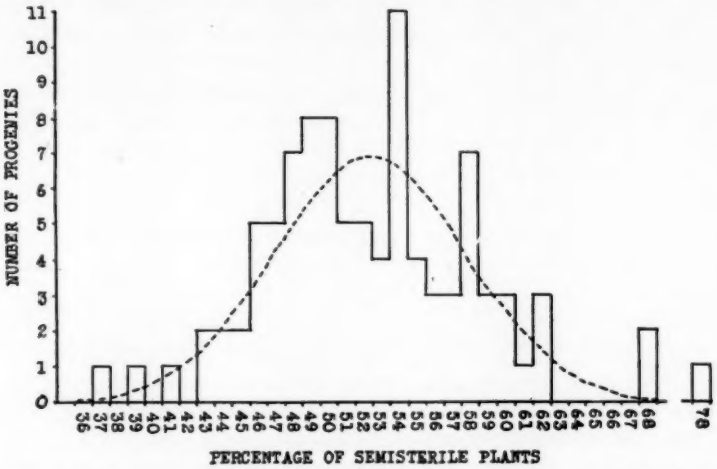

FIGURE 4.—Frequency distribution of segregating progenies with respect to percentage of semisterile plants. The broken line shows a normal curve of the same area and standard deviation.

DISTRIBUTION OF THE CHROMOSOMES IN THE RING AT THE REDUCTION DIVISIONS

On BELLING'S hypothesis of segmental interchange the breeding facts presented above may be interpreted to mean that in semisterile plants a terminal segment of one of the P-b_r chromosomes has exchanged position with a terminal segment of one of the l_g-v_4 chromosomes. The points of break are in the vicinities of the a_d and v_4 genes, respectively. The formation of a ring is accounted for on the assumption that the respective homologous ends of the two pairs of chromosomes concerned attract each other. On this hypothesis the modified and the normal chromosomes would be alternately placed in the ring as illustrated in figure 5, diagram 1.

Each of the two pairs of chromosomes involved in the semisterile-1 ring can frequently be recognized in both the diakinesis and equatorial plate stages on the basis of their size (figure 7). With respect to the plane of the equatorial plate the ring may become oriented on the spindle in two different ways. As shown in figure 5, diagram 1, the two smaller chromosomes may lie on one side of the equator (represented by the broken line) and the two larger ones on the other. According to the second alternative, illustrated in diagram 3 of the same figure, a small and a large chromosome lies on either side of the equator. If, in the separation of the chromosomes of the ring at anaphase, alternate chromosomes, a, b and a′b′, following

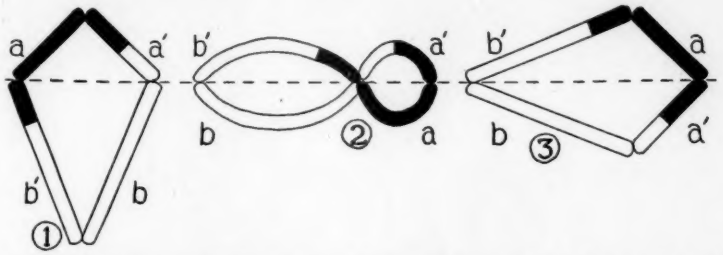

FIGURE 5.—Diagrammatic representation of the assumed constitution of the chromosome ring in semisterile-1 plants on the basis of segmental interchange. One end of chromosome a has interchanged with an end of chromosome b. The ring is oriented on the equatorial plant so that, 1, adjacent chromosomes of the same size, 2, alternate chromosomes and 3, adjacent chromosomes of unlike size pass to the same pole.

either mode of orientation, go to the same poles functional spores will result since each daughter nucleus receives a full complement of the hereditary materials involved (figure 5, diagram 2). Half the spores will receive the two modified chromosomes, a′b′, and the other half, the two normal ones, a, b. If, on the other hand, following either type of arrangement on the spindle, adjacent chromosomes accompany each other to the poles each of the resulting nuclei will not only receive some chromosome part in duplicate but will also lack a segment. Being deficient for certain genes, all the resulting spores, presumably, will abort.

Cytological examination of the semisterile-1 material shows clearly that either the adjacent or the alternate members of the chromosome ring may go to the same pole. When the former type of distribution occurs the two larger chromosomes may accompany each other and, likewise, the two smaller (figure 5, diagram 1). Or, one large and one small chromosome may go to each pole as would be expected if the plane of division is as repre-

sented by the broken line in figure 5, diagram 3. In other words, the different possibilities outlined in the preceding paragraph in regard to the distribution of the chromosomes in the ring are actually realized.

FIGURE 6.—Lateral views of equatorial plate stages showing the semisterile-1 ring. A. Chromosomes of similar size going to the same pole. B. Chromosomes of unlike size probably going to the same pole. C. Ring dividing so that alternate chromosomes are going to the same pole. ×2900.

That this is the case may be seen from figures 6 and 7. In figure 6, diagram A shows the members of the ring being distributed in such a way as

to separate the two larger chromosomes from the two smaller. In diagram B, adjacent chromosomes of different sizes are passing to the same poles. In C, alternate chromosomes of the ring are directed toward each pole of the spindle. These relations are further illustrated in figure 7. In diagram A, adjacent chromosomes of similar size are assorting together

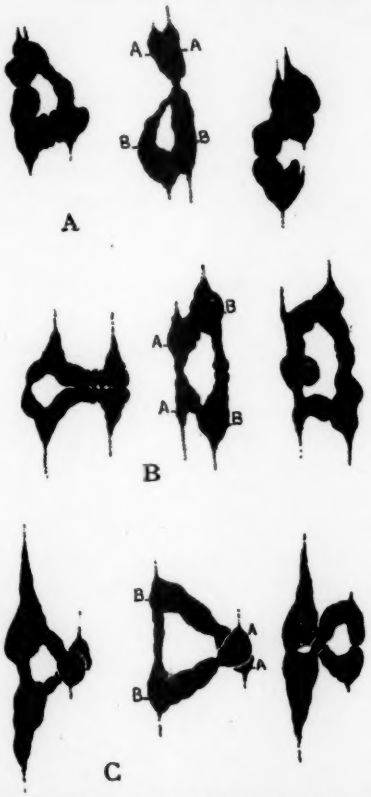

FIGURE 7.—Chromosome rings from equatorial plates showing types of distributions of the constituent chromosomes. A. Adjacent chromosomes of similar size, AA and BB, going to the same pole. B. Adjacent chromosomes of different size, AB, going to the same pole. C. Alternate chromosomes AB going to the same pole. ×2900.

whereas in B the plane of division is separating adjacent chromosomes of unequal size. In the three groups shown in diagram C alternate, rather than adjacent, chromosomes are passing to the same pole.

As discussed in a previous section, almost exactly one-half the pollen

grains and ovules in semisterile plants abort. While more material would have to be examined in order to get an adequate statistical representation of the cytological facts, it would appear that the chromosomes in the ring are distributed two by two at random. In half the cases alternate chromosomes go to the same pole leading to the formation of functional spores. In the remainder of the cases adjacent chromosomes assort together, the plane of division passing through the ring in each of the two possible ways with equal frequency.[6]

EFFECT OF SEMISTERILITY ON CROSSING OVER

It has been shown (tables 2, 7, 8, 9, 10, 11, 15, and 16) that crossing over occurs in the two pairs of chromosomes concerned in semisterility. Where two loci have been followed simultaneously in these chromosomes the effect of semisterility on the amount of recombination may be studied.

From table 2 it may be noted that in five progenies segregating for semisterility, l_g and v_4 show 47.96 percent recombination. This is not very dif-

TABLE 21

Effect of semisterility on crossing over between l_g and v_4.

MATING	NUMBER OF OFFSPRING				PERCENTAGE RECOMBINATION
	L_gV_4	l_gV_4	L_gv_4	l_gv_4	
Heterozygote normal					
L325-19×R490-20	111	96	68	98	43.96
L325-24×R490-92	133	65	109	97	43.07
L325-16×R493-100	100	94	58	97	43.55
		Unweighted average			43.53
Heterozygote semisterile					
L325-13×R489-91	75	65	60	68	42.91
L325-14×R493-41	107	104	47	92	43.14
L325-20×R491-54	67	56	87	105	45.39
R489-91×L325-13	79	63	67	78	45.29
R492-44×L326-5	76	40	41	64	36.65
R493-48×L326-10	61	51	47	51	46.86
R493-114×L326-10	67	48	39	55	41.62
		Unweighted average			43.12

ferent from the value, 43.2 percent, which DEMEREC (1924) obtained with normal (that is, not semisterile) plants. In order to check the point

[6] Since this manuscript was written, Doctor BARBARA MCCLINTOCK (1930) has brought forward cytological proof that semisterile-2 in maize involves an interchange of segments between the second and third smallest chromosomes. It is also shown, as in semisterile-1 discussed above, that the chromosomes in the semisterile-2 ring pass two by two to the poles apparently at random.

more closely, minimizing the possible influence of differences in the residual heredity, a series of $L_g\ V_4 \cdot l_g\ v_4$ plants in four sib progenies, R490, R491, R492 and R493 segregating semisterility, l_g and v_4 were mated with a normal $l_g\ v_4$ stock. Seven of the $L_g\ V_4 \cdot l_g\ v_4$ individuals used were semisterile and three were normal. The progenies were grown in the greenhouse and classified in the seedling stage. It will be seen in table 21, where the results are presented, that the average amount of recombination between l_g and v_4 among the offspring of the semisterile plants is 43.12 percent and in the progenies of the normal individuals 43.53 percent. These values are very close.

An important conclusion which follows from these facts is that a definite answer to one of the principal questions under consideration regarding semisterility, namely, the positions of the breaks in the two affected chromosomes, can probably be gained by the linkage method employed in this investigation. From the fact that semisterility has no influence on crossing over in the l_g-v_4 region, however, it does not necessarily follow that other regions of the chromosome are unaffected. There are reasons for thinking that, as the point of break is approached, crossing over may be interfered with. Particularly may this be true in the translocated chromosome parts (compare MULLER 1928). Through comparison with data from normal plants, however, the exceptional crossover values given by semisteriles may in themselves aid in locating the translocation loci. The significant fact now in hand is that semisterility affects crossing over in a considerable part of the b-l_g chromosome not at all.

The data relating to the distribution of fine-striped and brachytic, two genes borne by the other chromosome concerned in semisterility, point to the same conclusion. In the progenies segregation for semisterility f and b_r gives 4.69 percent recombination on the average (table 11). According to the unpublished results of EMERSON and of BRUNSON these genes show 5.4 percent crossing over in normal plants. Considering the fact that the results are based on different stocks these values may signify no real difference.

THE X-NORMAL CLASS OF PLANTS FROM SEMISTERILE-1

It was shown in an earlier paper (BRINK and BURNHAM 1929) that 25 percent of the offspring of selfed semisterile-1 individuals constitute a new class of fertile plants which gives all semisteriles when crossed with the original normal type. On the segmental interchange hypothesis these plants, called x-normals, are homozygous for the double translocation. The x-normal class is indistinguishable in its gross features at least from ordi-

nary maize plants of comparable breeding. The possibility of there being slight differences in maturity, plant size and ear size is under investigation but it may be said now that if such differences exist they are too small to be easily perceived. The x-normal individuals are vigorous, of apparently normal morphology and produce full and well developed ears.

The occurrence of x-normal plants apparently indistinguishable in form and fertility from the o-normal type in a regular proportion among the offspring of selfed semisteriles shows that the interchange of segments between non-homologous chromosomes assumed to account for the sterility does not alter the course of development when the modified chromosomes are present in homozygous condition. The genetic complex appears to function in the same way whether the chromosome parts in question are in the new position or in the old. The proportion of semisterile and normal offspring from normal ♀×semisterile ♂ matings points to the same conclusion. The two classes of individuals, normal and semisterile, from such a combination are produced through fertilization of normal eggs by normal and "semisterile-producing" sperm, respectively. These two types of sperm are transmitted through the male gametophyte which, in the seed plants, undergoes an appreciable vegetative development and is responsive in some degree to the genic complement which it carries (BRINK 1925). The results from three progenies bred in this way are at hand. In a total of 624 plants, 326 were semisterile and 298 normal. There is a small excess of semisteriles, but the deviation, 14 ± 8.42 plants, is within the limits of random sampling. Male gametophytes carrying the semisterile complex, therefore, develop as effectively as do normal male gametophytes.

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DISCUSSION AND SUMMARY

The foregoing studies show that semisterile-1 when tested with genes in the nine linkage groups recognized in maize assorts independently of seven of them but displays linkage with certain genes in the other two. Presumably the tenth group, which has not yet been established and hence can not be examined, is unaffected by semisterility.

BURNHAM (1929) has shown that semisterile-1 plants at diakinesis form eight bivalent chromosomes and a group of four usually arranged in a ring.

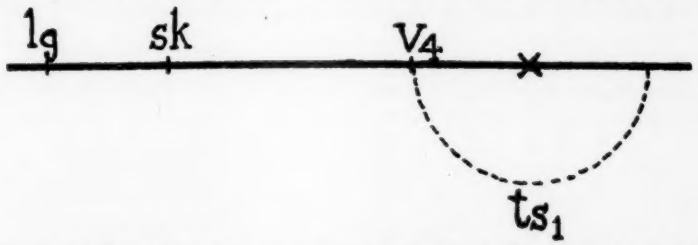

FIGURE 8.—Map of the l_g–v_4 chromosome showing the position of the assumed break (x) in relation to four genes with which semisterility was tested.

This observation has been amply confirmed in our own studies as may be seen from the figures. Normal plants and the x-normal type derived from semisteriles, on the other hand, show ten bivalent chromosomes at this stage. Evidently the changes leading to the union of two pairs of chromosomes in the ring structure are responsible for the partial sterility.

The chromosomes embodied in the ring are shown by the linkage tests reported in the present paper to be those corresponding to the *B*-l_g and *P*-b_r groups. In backcross matings involving genes in the former group, 11.6 percent recombination with semisterility was observed in the case of t_{s1}, 11.9 percent with v_4, 34.9 percent with s_k and 48.1 percent with l_g. The locus of t_{s1} in normal stocks has not been exactly determined although it is known to be in the v_4 end of the *B*-l_g chromosome. The order of the other three genes, however, is l_g-s_k-v_4. It is possible to compute from these facts the probable point at which the change in this chromosome concerned in semisterility has occurred. It is shown as x in the accompanying map. (figure 8).

In the *P-b*$_r$ group, *P* and *t*$_{s2}$, which are closely linked, gave 51.5 percent and 50 percent recombination, respectively, with semisterility. Brachytic and semisterility show 10.1 percent recombination while *f* and semisterility show 7.5 percent . In the normal plant the order of these genes has been demonstrated to be *P-b*$_r$-*f* with *t*$_{s2}$ adjacent to *P* on one side or the other. Anther ear (a_n) and adherent (a_d), whose exact positions in the *f* end of the chromosome remain uncertain, are found to be very closely associated with semisterility in inheritance. In backcrosses, anther ear shows 2.9 percent recombination with the semisterile condition and a_d gives 1.4 percent. These relations are epitomized in the accompanying map, x again denoting the probable position of the translocation locus (figure 9).

FIGURE 9.—Map of the *P–b*$_r$ chromosome showing the position of the assumed break (x) in relation to six genes with which semisterility was tested.

Further study of this material is being made with a view of determining whether the hypothesis of segmental interchange can be confirmed genetically. Only stocks in the x-normal condition can be used in this connection since a "false linkage" exists in semisterile plants between the genes in the two affected groups. (Compare BELLING 1925 and HAKANSSON 1929.) Moreover, it is necessary to have genes on both sides of the break in each chromosome in order to prove the interchange. Whether the present knowledge of the constitution of the *B-l*$_g$ and *P-b*$_r$ chromosomes in maize is sufficient for the purpose still remains to be determined. It is possible that in the case of the *B-l*$_g$ group that *t*$_{s1}$ is on the translocated piece. In the *P-b*$_r$ group it is not unlikely that either a_n or a_d or both are in the corresponding position. If it were shown, for example, that in the x-normal type *t*$_{s1}$ were linked with *f* and a_n or a_d linked with v_4, the evidence would be clear for segmental interchange.

Within the limits of random sampling 50 percent of the pollen from semisterile-1 plants is aborted. While the average amount of aborted pollen is almost exactly 50 percent, the deviations from this value in individual plants are slightly larger than would be expected to result from chance alone. If non-disjunction of one of the pairs in the ring occurred giving rise to gametes containing one normal and one modified chromosome the resulting 2n+1 plants would show a reduced degree of sterility.

Amounts of sterility significantly above 50 percent are more difficult to account for unless changes in additional chromosomes are assumed.

The two pairs of chromosomes entering into the formation of the ring are recognizably different in size and may frequently be distinguished at diakinesis and on the equatorial plate. This has enabled us to observe the manner in which the chromosomes in the ring assort at the first meiotic division. It is found that, in anaphase, either adjacent or alternate chromosomes may go to the same pole. When the former occurs, sometimes it is the chromosomes of similar size and sometimes those of different size which assort together. In either case the spores resulting should be nonfunctional since they are deficient for a segment of the one or the other chromosome. Functional spores follow the distribution of alternate chromosomes to the same pole. Fifty percent of these spores receive the two normal chromosomes and the remainder receive the two chromosomes with interchanged parts. It would appear from the pollen counts that in half the cases alternate chromosomes go to the same pole, in the other half, adjacent chromosomes assort together, it being entirely a matter of chance which two adjacent chromosomes separate from the ring together.

As a test of the proportion in which the two classes of functional spores, o-normal producing and x-normal producing, are formed by semisterile plants, the ratio of normal and semisterile plants in 97 progenies resulting from semisterile×normal matings was studied. The mean percentage of partially sterile plants in these families is found to be 52.35. This value is not significantly different from 50.00 percent and it may be concluded that, within the limits of random sampling, one half the spores which are capable of developing into gametophytes carry the normal chromosome complement while the other half possess the chromosome configuration causing the sterility.

It is shown that semisterility does not affect crossing over in the l_g-v_4 region of the b-l_g chromosome. In semisterile plants segregating for f and b_r about 4.7 percent recombination between these genes is found. This is somewhat less than the value (5.4 percent) reported for this region in normal plants. The difference, however, may be due to the fact that the two results are based on unrelated stocks grown under different circumstances. The fact that the crossover values in the two chromosome pairs involved in the ring are normal to within at least 10 units of the apparent points of break shows that the position of the latter may be determined with a fair degree of accuracy by linkage tests.

The plants, termed x-normal, which are homozygous for the condition leading to semisterility, appear to be normal in form and are apparently

fully fertile. The possibility of there being slight differences in these regards is being studied further but any variation that may exist is small. It would appear, therefore, that rearrangement of the chromosome parts assumed to account for the partial sterility does not alter the course of development in this particular case.

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TRANSLOCATIONS INVOLVING THE SECOND AND THE FOURTH CHROMOSOMES OF *DROSOPHILA MELANOGASTER*

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THE PROBLEM

Five translocations involving the third and the fourth chromosomes have been described in previous papers (DOBZHANSKY 1929a, 1930a). In each of these translocations, a section of the third chromosome was found to be broken and reattached to the fourth chromosome. The lengths of the broken off sections of the third chromosome were determined by cytological observations and were found to be different in each of the translocations. The lengths of the same sections were determined also by genetic methods and expressed in units of the map-distance. A cytological map of the third chromosome was constructed. The cytological map indicates the location of the observed points of breakage as seen in the chromosome under the microscope. The comparison of the cytological map with the regular genetic map of the same chromosome revealed two facts. First, the linear order of the genes is the same in both maps, and, second, the relative distances between the genes on the cytological map are in some cases much longer, and in other cases much shorter than suggested by the genetic map. The genes located in the middle region of the third chromsome are represented by the genetic map as lying too close to each other, while the relative distances between the genes lying in the ends of the chromosome are exaggerated by the genetic map. This discrepancy is apparently due to the lower frequency of crossing over per unit of the absolute distance at the middle of the length of the chromosome, as compared with its frequency at the ends of the chromosome.

The main purpose of the present work was to secure data for the construction of a cytological map of the second chromosome of *Drosophila melanogaster*. Furthermore, the phenomenon of translocation presents unique opportunities for the study of the mechanism of conjugation, crossing over, and reduction of chromosomes. Accumulation of data bearing on these questions is very desirable. Attention is, therefore, paid also to this side of the problem.

The work was done at the CALIFORNIA INSTITUTE OF TECHNOLOGY, in Pasadena. The author wishes to express his obligations to Doctors T. H. MORGAN and A. H. STURTEVANT for their advice and criticism.

ORIGIN OF THE TRANSLOCATIONS

The first translocation described in the literature (BRIDGES 1923), and certain translocations found since then (STERN 1926, STURTEVANT and DOBZHANSKY 1930), appeared spontaneously. More recently it was discovered by MULLER (1928) that the frequency of translocations rises very considerably in the progeny of flies treated by X-rays. The discovery of MULLER has made it practicable to attempt to get at will translocations involving any two of the chromosomes.

Since the basic object of the present work was to secure information concerning the cytological map of the second chromosome of Drosophila, the experiment was planned primarily for obtaining translocations involving the second and the fourth chromosomes. For the purpose just stated such translocations are superior to those involving the second and any other chromosome. An attachment of even a very small section of the second chromosome to the very small fourth chromosome may be expected to produce cytologically visible changes in the length of the fourth chromosome. The addition of a section of the same size to any of the other chromosomes, which are much longer than the fourth, may be cytologically invisible.

The usual method of finding translocations is based on the appearance of an apparent linkage of genes located in chromosomes involved in translocations (this method is described in detail by MULLER and ALTENBURG 1930, and DOBZHANSKY 1930a). Young wild-type males (from the "Oregon" stock) were treated by X-rays. The dosage was as follows: 50 kv peak, 5 ma, duration 60 minutes, distance 16 cm from the anticathode, 1 mm aluminum filter. Irradiated males were crossed in individual cultures to untreated females having the constitution $\frac{e_v}{e_v} \frac{C_v\ p_r}{a_l\ d_p\ b\ p_r\ c\ p_z\ s_p}$[1]. In the

[1] These females are homozygous for the fourth-chromosome gene eyeless (e_v). One of their

F_1 generation wild-type males were selected, and backcrossed in individual cultures to $\frac{e_y}{e_y}\ \frac{C_y\ p_r}{a_l\ d_p\ b\ p_r\ c\ p_x\ s_p}$ females. These wild-type males, according to their pedigree, have the constitution $\frac{e_y}{+}\ \frac{a_l\ d_p\ b\ p_r\ c\ p_x\ s_p,}{+}$ that is, they received an untreated fourth chromosome carrying e_y, and an untreated second chromosome carrying $a_l\ d_p\ b\ p_r\ c\ p_x\ s_p$ from their mothers, and a treated fourth chromosome and a treated second chromosome carrying the wild-type allelomorphs of the genes just mentioned from their fathers.

In an experiment arranged in the fashion just described it is possible to discover only those translocations which involve the treated second, fourth, and Y-chromosomes. If no translocations involving these chromo-

TABLE 1

Cultures showing linkage of genes located in different chromosomes.

Progeny of the cross $\frac{+}{e_y}\ \frac{+\ +\ +\ +\ +\ +\ +\ +}{a_l\ d_p\ b\ p_r\ c\ p_x\ s_p}$ ♂ × $\frac{e_y}{e_y}\ \frac{+\ +\ C_y\ +\ p_r\ +\ +\ +}{a_l\ d_p\ +\ b\ p_r\ c\ p_x\ s_p}$ ♀

CULTURE NUMBER	TRANSLOCATION	WILD-TYPE		e_y		$a_l\ d_p\ b$ $p_r\ c\ p_x$ s_p		$a_l\ d_p\ b$ $p_r\ c\ p_x$ $s_p\ e_y$		C_y		$C_y\ e_y$		$C_y\ p_r$		$C_y\ p_r$ e_y		MINUTE p_r		$a_l\ d_p\ b$ $c\ p_x\ s_p$	
		♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
6575	a	4	4	..	..	..	..	2	4	7	5	..	..	..	..	6	5	..	..	..	..
7781	b	13	9	..	..	..	..	4	2	18	14	..	..	..	..	15	8	..	..	..	..
7718	c	11	17	..	..	..	..	8	6	8	11	..	..	..	..	18	5	..	..	..	..
7691	d	12	9	..	..	..	..	4	3	7	12	..	..	..	..	16	5	..	..	..	..
6304	A	..	9	..	9	4	..	3	..	..	9	..	9	11	..	7	..	..	..	..	..
6370	B	..	6	..	4	6	..	5	..	..	7	..	2	4	..	1	..	..	..	..	..
7617	C	..	26	..	33	14	..	21	..	..	22	..	32	27	..	26	..	..	..	..	..
7573	D	..	22	..	16	7	..	13	..	..	11	..	17	14	..	11	..	..	..	..	..
7628	E	..	15	..	19	13	..	9	..	..	19	..	16	12	..	15	..	..	..	..	..
7681	F	..	16	..	11	9	..	7	..	..	25	..	12	17	..	13	..	..	..	..	..
7831	G	..	10	..	8	8	..	4	..	..	15	..	21	16	..	11	..	..	..	..	5
7810	H	..	9	..	8	6	..	6	..	..	29	..	20	8	..	11	..	2	..	..	13
7832	I	..	4	..	5	2	..	1	..	..	9	..	10	9	..	6	..	..	..	..	..
7748	J	..	29	..	27	19	..	11	..	..	22	..	16	23	..	23	..	..	..	..	..

second chromosomes carries the dominant gene Curly (C_y), the recessive purple (p_r), and the inverted sections $C_{II\ L}$ and $C_{II\ R}$ (not shown in the above given formula) which prevent most crossing over in the second chromosome. The other second chromosome carries the recessive genes aristaless (a_l), dumpy (d_p), black (b), purple (p_r), curved (c), plexus (p) and speck (s_p).

I am greatly obliged to Doctor H. J. MULLER who kindly placed this stock at my disposal.

somes occur, sixteen classes of offspring are expected in the next generation (the first sixteen classes shown in table 1). If a translocation involving the second and the fourth chromosomes takes place, only eight classes of offspring appear, since the other eight classes, representing the recombinations of the second- and the fourth-chromosome characters, must be either inviable or possess visible external abnormalities. Likewise, if a translocation involving the second and the Y-chromosome occurs (that is, if a section of the second chromosome becomes attached to the Y-chromosome), eight classes of offspring representing the recombinations of sex and the second-chromosome characters may be expected to be missing or visibly abnormal.

Out of 551 cultures, 412 cultures gave the normal result (that is, free recombination of sex, the second- and the fourth-chromosome characters), 125 cultures were sterile, 4 cultures (numbers 6575, 7781, 7718, 7691, see table 1) gave no recombination of the fourth-chromosome and the second chromosome characters, and 10 cultures (the rest of the cultures shown in table 1) gave no recombination of sex and the second-chromosome characters.

Wild-type males from each of the four cultures, which gave no recombination of e_y and the second-chromosome characters, were crossed separately to $\frac{e_y}{e_y} \frac{C_y \; p_r}{a_l \, d_p \, b \, p_r \, c \, p_z \, s_p}$ females. The apparent linkage of the fourth-chromosome and the second-chromosome characters persisted in the next generation, confirming the presence of translocations involving chromosomes II and IV. By repeating this mating in each generation, four lines were established, which were designated as translocation II-IVa, II-IVb, II-IVc, and II-IVd respectively (see table 1).

Wild-type males from each of the ten cultures which gave no recombination of sex and the second-chromosome characters were crossed to homozygous $a_l \, b \, c \, s_p$ females. Mostly wild-type males and $a_l \, b \, c \, s_p$ females were produced. Translocations involving chromosomes II and Y are, therefore, present in these cultures. By mating wild-type males to $a_l \, b \, c \, s_p$ females in each generation, ten separate strains were established, which were designated as translocation II—Y A, B, C, D, E, F, G, H, I, J respectively (see table 1).

The present paper gives an account of the results of the investigation of the translocations involving chromosomes II and IV. Those involving chromosomes II and Y have been briefly described (DOBZHANSKY 1930b) and will be described in more detail later.

LOCI AT WHICH THE SECOND CHROMOSOME IS BROKEN IN TRANSLOCATIONS

The apparent linkage of genes located in the second and in the fourth chromosomes may be explained on four different assumptions. First, both chromosomes involved in a translocation may fuse together to form one compound chromosome. Second, a section of the second chromosome may become broken off, and reattached to the fourth chromosome. Third, a section of the fourth chromosome may be broken off, and attached to the second chromosome. Fourth, both the second and the fourth chromosomes may be broken each into two fragments, and the four resulting fragments may reunite in a new way, to form two "new" chromosomes. If the first assumption is true, the genes of the second and of the fourth linkage groups lie in the same chromosome, and the linkage observed in translocations is a real linkage. If the second, the third, or the fourth assumption is true, we are dealing with an apparent linkage; for in these cases gametes carrying recombinations of the genes belonging to the second and to the fourth linkage groups may be formed, but these gametes must carry either a duplication or a deficiency for a section of one of the chromosomes involved in the translocation, and may, therefore, give rise to inviable zygotes.

The first assumption may be considered very improbable. The fusion of the second and the fourth chromosomes would result in the formation of a chromosome having two spindle-fibre attachments (each of the chromosomes fused contributing one attachment). No translocations leading to formation of chromosomes having none or more than one spindle-fibre attachment are described in the literature, and one may suppose that, at least in Drosophila, such chromosomes are unable to behave normally at mitosis, and are, therefore, eliminated.

The third assumption is also improbable. If a section of the fourth chromosome is attached to the second chromosome, some gametes carrying a duplication or a deficiency for this section must be formed in flies carrying translocations. Since individuals having a deficiency or a duplication for the whole fourth chromosome are known to be viable and distinct in appearance from normal flies (BRIDGES 1921), one may suppose that gametes carrying a duplication or a deficiency for a part of the fourth chromosome will give rise to viable zygotes. Hence, some recombination of the second- and the fourth-chromosome characters would appear in the progeny of such translocations. No such recombination-classes are, however, found. This evidence is, of course, not entirely conclusive, because hypo- or hyperploidy for a section of a chromosome may in some cases be more del-

eterious than hypo- or hyperploidy for the whole of this chromosome (intrachromosomal unbalance, MULLER 1930a).

There remain, therefore, the second and the fourth assumptions, the former being apparently more probable than the latter since a breakage of the fourth chromosome has never been demonstrated.

The locus of attachment of the fourth chromosome to the second (which is also the locus at which the second chromosome was broken) may be determined by a linkage experiment. Indeed, if a female fly carrying a translocation is heterozygous for a second-chromosome gene a, and for a fourth-chromosome gene b, the frequency of recombination of a and b indicates the distance between a and the locus of breakage. (For a more detailed discussion of this method of determination of the locus of breakage see DOBZHANSKY 1930a).

Wild-type males from each of the cultures in which II-IV translocations were found (see table 1) were crossed to homozygous $e_v\ a_l\ d_p\ b\text{-}p_r\ c\ p_z\ s_p$ females. In F_1 wild-type females were selected and backcrossed to $e_v\ a_l\ d_p\ b\ p_r\ c\ p_z\ s_p$ males. These wild-type females have the constitution $\frac{+^{e_v}}{e_v\ a_l\ d_p\ b\ p_r\ c\ p_z\ s_p}$, that is, they are heterozygous for the translocation and for the recessive genes indicated (the second chromosome involved in the translocation is represented by a broken line). The results of this backcross are presented in tables 5–8 (see Appendix). The calculated crossing-over values for each of the four translocations studied are presented in table 2.

As shown in table 2, in each of the four translocations the fourth-chromosome gene e_v seems to occupy a different locus among the second-chromosome genes. That is to say, in each of the translocations the second chromosome has been broken at a different locus. In b-translocation the breakage took place in the a_l-d_p interval, in c-translocation in the d_p-b interval, in a-translocation in the p_r-c interval, and in d-translocation in the $c-p_z$ interval. The position of these genes, as well as of the breakage points, on the genetic map of the second chromosome is shown in diagram 2.

An examination of table 2 shows, furthermore, that the frequency of crossing over in the same interval may be very different in different translocations. In order to get a standard of comparison for the crossing-over values observed in the translocations, a control experiment was undertaken. Wild-type "Oregon" males were crossed to $e_v\ a_l\ d_p\ b\ p_r\ c\ p_z\ s_p$ females, and wild-type females which appeared in F_1 were backcrossed to $e_v\ a_l\ d_p\ b\ p_r\ c\ p_z\ s_p$ males. Two thousand one hundred ten flies were ob-

tained in the next generation; the crossing-over values observed in these counts are presented in table 2.

TABLE 2

Crossing-over values for the intervals studied in the second chromosome.

			Translocation a				
Interval	a_1–d_p	d_p–b	b–p_r	p_r–e_y	e_y–c	c–p_z	p_z–s_p
Value	10.6	30.75	8.6	1.75	0.1	4.8	3.75
			Translocation b				
Interval	a_1–e_y	e_y–d_p	d_p–b	b–p_r	p_r–c	c–p_z	p_z–s_p
Value	0.2	0.06	0.8	0.5	19.4	26.6	8.4
			Translocation c				
Interval	a_1–d_p	d_p–e_y	e_y–b	b–p_r	p_r–c	c–p_z	p_z–s_p
Value	0.3	0.1	9.5	6.1	26.4	30.3	6.9
			Translocation d				
Interval	a_1–d_p	d_p–b	b–p_r	p_r–c	c–e_y	e_y–p_z	p_z–s_p
Value	13.7	32.5	9.2	13.7	9.3	0.7	2.6
			Control experiment				
Interval	a_1–d_p	d_p–b	b–p_r	p_r–c	c–p_z	p_z–s_p	
Value	13.6	31.0	8.5	21.3	23.8	7.1	

In a- and in d-translocation the frequency of crossing over is strongly reduced in all intervals lying to the right of the gene p_r (see table 3), and is normal, or even slightly increased, in all intervals lying to the left of p_r. In

TABLE 3

Differences between the crossing-over values observed in the translocations and those observed in the control experiment.

INTERVAL	TRANSLOCATION				LIMB OF THE CHROMOSOME
	a	b	c	d	
a_1–d_p	−3.0	−13.3	−13.3	+0.1	
d_p–b	−0.2	−30.2	−21.4	+1.5	Left
b–p_r	+0.1	−8.0	−2.4	+0.7	
p_r–c	−19.5	−1.9	+5.1	−7.6	
c–p_z	−19.0	+2.8	+6.5	−13.8	Right
p_z–s_p	−3.3	+1.3	−0.2	−4.5	

b- and in c-translocation crossing over is scarce to the left of p_r, but it is normal to the right of p_r. It is known, however, that in a- and in d-translocation the second chromosome is broken to the right of p_r, and in b- and

in c-translocations the breakage occured to the left of p_r. That is to say, the reduction of the frequency of crossing over to the right or to the left of the p_r-locus is a function of the location of the breakage-point in respect to this gene. The strongest relative reduction of crossing over takes place in or at the interval in which the breakage-point lies (in the p_r-c interval in a-translocation, in the c-p_z interval in d-translocation). However in all four cases studied, the reduction of crossing over extends to the locus of p_r, but not beyond that locus. One may suppose that some point lying at or close to the p_r-locus is responsible for this phenomenon.

The behavior of the translocations under discussion is quite parallel to that of the III-IV translocations (DOBZHANSKY 1929a, 1930a). It has been shown there that crossing over is reduced in the whole limb of the V-shaped third chromosome in which the locus of breakage lies, but remains normal in the opposite limb. The point dividing the two limbs is the locus of the spindle-fibre attachment. One may suppose by analogy that the locus of p_r, dividing the second chromosome into two genetical "limbs" of approximately equal length (see diagram 2), lies at or close to the spindle-fibre attachment. This supposition is substantiated by independent evidence from several sources. BRIDGES and MORGAN (1923), studying the distribution of the double crossovers in the second chromosome, came to the conclusion that the attachment of the spindle fibre is located in the region of the genes black or purple. STURTEVANT (in press) came to the same conclusion on the basis of the study of the effects of the inverted sections of the second chromosome. STURTEVANT and DOBZHANSKY (1930, in press) found that the spindle fibre is probably attached at a point lying about 0.2 of a map-unit to the right of the gene Bristle (which is located 0.2 of a map-unit to the right of p_r). Finally, this was demonstrated genetically and cytologically on the basis of the study of II-Y translocations (a preliminary account, DOBZHANSKY 1930b). One may conclude that the genes p_r and B_1 are located in the chromosome close to the attachment of the spindle fibre.

The results of the study of crossing over in the second chromosome of the translocations (tables 2, 5–8) show that in all four cases studied the broken-off fragment of the second chromosome is attached to the fourth chromosome by its broken end, and not by its free end. The following reasoning shows how this conclusion is arrived at. Suppose the chromosome *abcdefgh*, having the spindle fibre attached at *h*, is broken between the loci of the genes *c* and *d*. The fragment *abc* is attached to another chromosome (symbolized by *M*, and, of course, having its own spindle fibre) by

its free end (the *a* end). An individual heterozygous for this translocation must be represented thus:

$$\frac{}{M} \quad \frac{\overline{M\ a\ b\ c} \quad \overline{d\ e\ f\ g\ h}}{a'\ b'\ c'\ d'\ e'\ f'\ g'\ h'}$$

Simple crossing over between the fragment *abc* and the normal chromosome *a' b' c' d' e' f' g' h'* leads to formation of chromosomes having two spindle fibres (chromosome *M a b c' d' e' f' g' h'*) and having no spindle fibre (chromosome a' *b' c*). Such chromosomes presumably are inviable, and, therefore, no simple crossing over between the fragment *abc* and the normal chromosome can be recovered. If, however, the fragment *abc* is attached by its broken end, so that an *abcM* chromosome is formed, simple crossing over between the fragment and the normal chromosome gives gametes which must produce viable zygotes. As shown in tables 5–8, simple crossing over occurs between the breakage point and both ends of the second chromosome in all translocations.

HOMOZYGOUS TRANSLOCATIONS

The above description dealt with the behavior of translocations in heterozygous form. Individuals heterozygous for the translocations must have, and, as will be shown below, do have, one normal second chromosome, one normal free fourth chromosome, and one second chromosome broken into two fragments, the shorter of which is attached to the other fourth chromosome. Individuals homozygous for the translocations must have no normal second or fourth chromosomes, but must have two pairs of "new" chromosomes. One of the "new" ones represents a fragment of the chromosome II attached to IV, and the other represents the remaining fragment of II retaining its spindle fibre.

As shown by MULLER and ALTENBURG (1930) and by DOBZHANSKY (1929b, 1930a), most of the translocations are, for some not yet exactly known reason, lethal when homozygous, or individuals homozygous for translocations are abnormal in appearance, sterile, and have low viability. Individuals heterozygous for translocations are in most cases quite normal in appearance and fully viable.

Flies were obtained which were heterozygous for the a-, b-, c,- and d-translocations respectively, and which carried in their normal (unbroken) second chromosome the dominant genes Curly and Lobe (*L*), and the crossover suppressors $C_{\text{II L}}$ and $C_{\text{II R}}$. Such flies, heterozygous for the same translocation, were mated to each other. Any wild-type individual appearing in the next generation must be homozygous for the respective

translocation. In case the homozygous translocation is fully viable, a ratio 2 C_y L:1 wild-type must be expected.

It was shown by this method that a-translocation apparently is always lethal when homozygous. In c- and in d-translocation homozygous individuals appear very rarely (less than 3 percent of the expected frequency). They are very weak, their wings usually do not unfold (in c-translocation) or are filled with liquid (in d-translocation), and they die soon after emergence. Both sexes presumably are completely sterile, although it is difficult to ascertain this point since they usually die before they mate. Only b-translocation is viable when homozygous, normal in appearance, and fully fertile in both sexes. It is, however, less vigorous than wild-type flies, since instead of the expected ratio 2 C_y L:1 wild-type a ratio approaching 3:1 is obtained.

The death of the individuals homozygous for c- and, especially, d-translocation takes place mostly in later stages of development. This is shown by the fact that the cytological study of the fully grown larvae from the mating translocation × translocation revealed the presence of many individuals homozygous for the translocations (see below).

NON-DISJUNCTION OF THE SECTIONS OF THE SECOND CHROMOSOME

A convincing proof of the presence of breakage in the second chromosome in translocations is provided by the phenomenon of non-disjunction of sections of this chromosome.

Individuals were obtained (see table 8) which were heterozygous for d-translocation, and which carried the genes p_z and s_p in the fragment of the second chromosome attached to the fourth, and the genes a_l and d_p in the other fragment of the second chromosome remaining free. The constitution of these individuals is represented in the upper part of diagram 1. At gametogenesis such individuals may produce six kinds of gametes, shown in diagram 1. At the reduction division, both fragments of the second chromosome involved in the translocation may pass to the same pole, the normal second chromosome going to the opposite pole. Gametes 1 and 2 (diagram 1) are formed in this way. Either fragment of the second chromosome may pass, however, to the same pole of the spindle together with the normal second chromosome. Gametes 3 to 6 are formed in this case.

If an individual of the constitution represented in diagram 1 is crossed to flies free from translocations, only gametes 1 and 2 give rise to viable zygotes. Gametes 4 and 6 produce zygotes carrying a duplication for a section of the second chromosome, while gametes 3 and 5 give rise to zy-

gotes deficient for a section of the same chromosome. Individuals possessing a deficiency or a duplication for a section of a chromosome are usually abnormal in appearance, and may be identified. No such individuals were, however, found in the progeny of d-translocation crossed to wild-type flies. Hence, these gametes either are not produced at all, or else give rise to inviable zygotes.

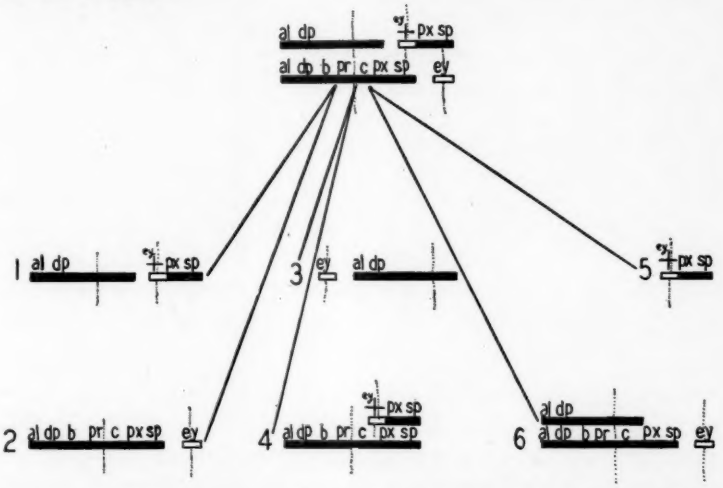

DIAGRAM 1.—Six kinds of gametes which may be produced in a fly heterozygous for d-translocation. Second chromosome—black, fourth chromosome white. Spindle fibres are indicated by dotted lines. 1 and 2—regular gametes, 3–6 non-disjunctional gametes. 3 and 5 gametes carrying a deficiency for a section of the second chromosome, 4 and 6—gametes carrying a duplication for a section of the second chromosome.

This alternative may be decided by mating two individuals heterozygous for the same translocation to each other. Each parent in this case may be supposed to produce the six kinds of gametes shown in diagram 1. If gamete 3 from one parent meets gamete 4 from the other parent, a viable zygote is produced, since these gametes are complementary to each other (deficiency is neutralized by the corresponding duplication). A viable zygote is also produced if gamete 5 meets gamete 6. As shown in table 4 the results of mating two individuals heterozygous for the translocation and having the constitution

$$\frac{a_l\ d_p}{a_l\ d_p\ b\ p_r\ c}\ \frac{+^{e_v}\ p_x\ s_p}{p_x\ s_p}\ \frac{\quad}{e_v} \times \frac{\quad}{C_v\ p_r}\ \frac{+^{e_v}}{\quad}\ \frac{\quad}{e_v}$$

must be the following: 1 wild-type: 3 C_v: 1 $C_v\ p_r\ e_v$: 1 $p_x\ s_p$: 1 $a_l\ e_v$ (pro-

vided all six kinds of gametes are produced in equal number). If the fragment of the second chromosome retaining its own spindle fibre (the $a_l\ d_p$

TABLE 4

Mating: $\frac{a_l\ d_p}{a_l\ d_p\ b\ p_r\ c\ p_z\ s_p}$ — e_y × $\frac{e_y}{C_y\ p_r}$ — e_y

	(1) a_l d_p $+^{e_y}$ p_z s_p	(2) e_y a_l d_p b p_r c p_z s_p	(3) e_y a_l d_p	(4) a_l d_p b p_r c p_z s_p $+^{e_y}$ p_z s_p	(5) $+^{e_y}$ p_z s_p	(6) e_y a_l d_p a_l d_p b p_r c p_z s_p
(1) $+^{e_y}$	Homozygous translocation (1)	Wild-type (2)	dies (3)	dies (4)	dies (5)	dies (6)
(2) $C_y\ p_r$ — e_y	C_y (7)	$C_y\ p_r\ e_y$ (8)	dies (9)	dies (10)	dies (11)	dies (12)
(3) e_y	dies (13)	dies (14)	dies (15)	$p_z\ s_p$ (16)	dies (17)	dies (18)
(4) $+^{e_y}$ $C_y\ p_r$	dies (19)	dies (20)	C_y (21)	dies (22)	dies (23)	dies (24)
(5) $+^{e_y}$	dies (25)	dies (26)	dies (27)	dies (28)	dies (29)	$a_l\ d_p$ (30)
(6) $C_y\ p_r$ — e_y	dies (31)	dies (32)	dies (33)	dies (34)	C_y (35)	dies (36)

fragment, diagram 1) always passes to the opposite pole from the normal second chromosome at the reduction division, no gametes 5 and 6 will be produced. In this case the expected ratio is L wild-type: 2 C_y: 1 $C_y\ p_r\ e_y$: 1

$p_z\ s_p$. If no non-disjunction takes place the expected ratio is 1 wild-type: 1 C_v:1 $C_v\ p_r\ e_v$ (compare table 4). The results obtained in the experiment are:

	Wild-type	C_v	$C_v\ p_r\ e_v$	$p_z\ s_p$	$a_l\ d_p$	Homozygous translocation
Observed	225	459	182	236	..	3
Expected (*1:2:1:1*)	*220.4*	*440.8*	*220.4*	*220.4*	..	..

It may be concluded that in d-translocation gametes 1, 2, 3 and 4 are formed in approximately equal numbers, and gametes 5 and 6 are very seldom if ever formed. That is to say, the fragment of the second chromosome attached to the fourth is distributed at random with respect to the normal second chromosome at the reduction division. The deviation from the expected ratio is due, probably, to the lower viability of the e_v-carrying class.

Similar experiments were performed also for a-, b- and c-translocation. Individuals heterozygous for a-translocation and having the constitution:

$$\frac{a_l\ d_p \quad +^{e_v}}{a_l\ d_p\ b\ p_r\ c\ p_z\ s_p} \quad \frac{\quad}{e_v} \times \frac{\qquad +^{e_v}}{C_v\ \ p_r} \quad \frac{\quad}{e_v}$$

were mated together. The expected ratios in this case are (compare table 4) 2 wild-type:3C_v:1 $C_v\ p_r\ e_v$:1 $a_l\ d_p$ (in case all six kinds of gametes are produced), or 2 wild-type:2 C_v:1 $C_v\ p_r\ e_v$ (in case gametes 5 and 6 are not produced), or 1 wild-type:1C_v:1 $C_v\ p_r\ e_v$ (in case no non-disjunction takes place). The results obtained are:

	Wild-type	C_v	$C_v\ p_r\ e_v$	$a_l\ d_p$
Observed	891	863	375	..
Expected (*2:2:1*)	*851.6*	*851.6*	*425.8*	..

One may conclude that in a-translocation the fragment of the second chromosome attached to the fourth is independent of the normal second chromosome at the reduction division, but no non-disjunction of the fragment of the second chromosome retaining its own spindle fibre takes place.

Individuals heterozygous for c-translocation and having the constitution

$$\frac{+^{e_v} \quad b\ p_r\ c\ p_z\ s_p}{a_l\ d_p\ b\ p_r\ c\ p_z\ s_p} \quad \frac{\quad}{e_v} \times \frac{+^{e_v}}{\qquad} \quad \frac{\quad}{e_v}$$

were crossed to each other. Here the expected ratio is 5 wild-type:1e_v:1 *b*-

$p_r\ c\ p_z\ s_p$ (in case all six kinds of gametes are formed), or 4 wild-type:1 e_v (in case the fragment of the second chromosome retaining its own spindle fibre undergoes no non-disjunction), or 2 wild-type:1 e_v (if no non-disjunction takes place). The observed ratio is:

	Wild-type-	e_v	$b\ p_r\ c\ p_z\ s_p$	Homozygous translocation
Observed	975	224	..	5
Expected (*4:1*)	*959.2*	*239.8*	..	..

It follows that in c-translocation the fragment of the second chromosome attached to the fourth is independent of the normal second chromosome at the reduction division, but the fragment of the second chromosome retaining its spindle fibre does not undergo non-disjunction.

In b-translocation, individuals carrying a duplication for a section of the second chromosome survive under certain conditions. If a male heterozygous for b-translocation and heterozygous for $e_v\ a_l\ d_p\ b\ p_r\ c\ p_z\ s_p$ is crossed to $e_v\ a_l\ d_p\ b\ p_r\ c\ p_z\ s_p$ females (free from translocation) only wild-type and $e_v\ a_l\ d_p\ b\ p_r\ c\ p_z\ s_p$ offspring are produced. Here individuals carrying the duplication do not survive, presumably because of the decrease of viability produced by the second-chromosome recessive genes just indicated. If, however, the same males are crossed to $a_l b\ s_p$ females (free from translocations), some individuals carrying a duplication survive. In a cross of the nature just indicated there were obtained:

Wild-type	$a_l\ b\ s_p$	$b\ s_p$ (duplication)
768	713	315

The $b\ s_p$ individuals are, evidently, carrying a duplication for a section of the second chromosome including the gene aristaless (they have two doses of a_l, but the manifestation of a_l is nearly completely suppressed by its normal allelomorph). These individuals are different in appearance from normal flies. They have short and plump bodies, the dorsal surface of the abdomen is flattened, the eyes are strongly convex, the wings are expanded and curved (sometimes resembling the mutation curved), the scutellar bristles are often erect (this character is, probably, due to incomplete suppression of a_l), their development is slow, they have low viability, and are sterile in both sexes. As shown above, in b-translocation the second chromosome is broken between the genes a_l and d_p, and the fragment carrying a_l is attached to the fourth chromosome. The $b\ s_p$ individuals just described carry, therefore, a duplication for a section of the second chromosome in-

cluding a_l, but not including d_p or any other second-chromosome gene located to the right of d_p.

Individuals heterozygous for b-translocation and having the constitution

$$\frac{+^{e_y} \quad c\ p_z\ s_p}{a_l\ d_p\ b\ p_r\ c\ p_z\ s_p} \quad \frac{}{e_y} \times \frac{+^{e_y}}{C_y\ p_r} \quad \frac{}{e_y}$$

were mated together. This cross may give the following results. The ratio 3 wild-type:3 C_y:1 $C_y\ p_r\ e_y$:1 $c\ p_z\ s_p$ must be produced if both fragments of the second chromosome involved in the translocation are distributed at random (it has to be taken into account that in b-translocation the individuals homozygous for the translocation survive, compare table 4). If only the fragment of the second chromosome attached to the fourth undergoes non-disjunction, a ratio 3 wild-type:2 C_y:1 $C_y\ p_r\ e_y$ is expected. If no non-disjunction takes place the ratio 2 wild-type:1 C_y:1 $C_y\ p_r\ e_y$ is expected. The results of the experiment are:

	Wild-type	C_y	$C_y\ p_r\ e_y$	$c\ p_z\ s_p$	Duplication
Observed	976	761	448	..	83
Expected (*3:2:1*)	*1092*	*729*	*364*	..	..

The agreement of the observed results with the expectation here is less close than was obtained in other translocations. This may be due, first, to the lower viability of the homozygous translocation as compared with heterozygous (this produces a decrease of the wild-type class), and, second, to the not quite random distribution of the fragment of the second chromosome attached to the fourth at the reduction division (this produces an increase of the $C_y\ p_r\ e_y$ class). It is certain in any case that no non-disjunction of the fragment of the second chromosome retaining its own spindle fibre takes place in b-translocation.

The data presented in this chapter show, therefore, that in all four II-IV translocations studied the section of the second chromosome retaining its own spindle fibre always goes to the opposite pole from the normal second chromosome at the reduction division. On the other hand, the section of the second chromosome attached to the fourth is distributed at random in respect to the normal second (except, possibly, in b-translocation). These results might give rise to a supposition that the disjunction of chromosomes at the reduction division is determined simply by their spindle fibres, that is, that the points of the attachment of the homologous spindle fibres always pass to the opposite poles at the reduction division.

Facts are known that disprove this supposition. In translocations in-

volving chromosomes III and IV (DOBZHANSKY 1930a), the general nature of which is very similar to that of the II-IV translocations described here, the fragment of the third chromosome attached to the fourth is not distributed at random in respect to the normal third chromosome, but passes to the opposite pole from it at the reduction division more frequently than it passes to the same pole. On the other hand, the section of the third chromosome retaining its own spindle fibre sometimes passes to the same pole with the normal third chromosome. MULLER (1930b) described a translocation involving a transfer of a rather short section of the third chromosome onto the second chromosome. As shown by MULLER, the section of the third chromosome attached to the second usually passes to the opposite pole from the normal third chromosome at the reduction division. The section of the third chromosome retaining its own spindle fibre in MULLER's case does not undergo non-disjunction.

There exist reasons for supposing that one of the factors determining the disjunction of sections of chromosomes involved in translocations is the relative lengths of these sections. The influence of the spindle fibres is a phenomenon of rather secondary importance. STURTEVANT and DOBZHANSKY (1930, also data in press) and KARPECHENKO (unpublished) have shown that in translocations in which the second and the third chromosomes have exchanged sections the length of which equals approximately one-half of the length of either chromosome, all four resulting fragments undergo non-disjunction equally frequently. The influence of the spindle fibres in these cases seems to be nil. If, however, the exchanged sections are not equal in length, the shorter sections undergo non-disjunction more frequently than the longer sections. As soon as the difference in the relative length of the exchanged sections becomes great enough, the longer sections do not undergo non-disjunction at all, and the shorter sections are distributed more or less at random in respect to their homologues.

In II-IV translocations described in this paper the sections of the second chromosome transposed onto the fourth chromosome are mostly shorter than the sections of the third chromosome involved in the III-IV translocations referred to above. This fact may, at least partly, account for the difference in behavior between the II-IV and the III-IV translocations

CYTOLOGY OF THE TRANSLOCATIONS

Two methods were applied for the study of the chromosomes in the translocations, namely the investigation of the oögonial divisions in ovaries of freshly hatched adult females, and of the cell divisions in the nerve-ganglia of larvae. For the investigation of the oögonial divisions,

ovaries of females heterozygous for the translocations were fixed successively in strong Flemming's fluid (1 hour) and in 1 percent solution of chromic acid (20–24 hours). The 5μ thick sections were stained in iron haematoxylin. For the investigation of the nerve-cell divisions males and females heterozygous for the translocations and for the gene C_y were mated together. One-half of the individuals in the progeny of this mating are heterozygous for the translocation, one-quarter may be homozygous for the translocation, and one-quarter die in early stages of development because of the lethal effect of the gene lying in the C_y chromosome. The nerve ganglia of larvae appearing in these cultures were dissected and fixed in strong Navashin's fluid. The 7μ sections were stained in gentian-violet (gentian-violet-KKI-clove oil method).

The chromosomes do not appear the same in the oögonial divisions (plate 1, figures 1–12) and in the nerve-cell divisions (plate 1, figures 13–18, plate 2 figures 19–32). The oögonial chromosomes are rather short and thick, exhibit a strong tendency toward somatic pairing, and the constrictions are usually not very strongly pronounced. The chromosomes in the nerve-cells are considerably longer and more slender than the oögonial chromosomes and lie far apart from each other, somatic pairing being as a rule rather weak. The chromosomes frequently are bent, and the different parts of the same chromosome frequently lie in different planes. The constrictions are usually strongly pronounced. Sometimes certain of the constrictions are so strong that the chromosome seems to be broken into fragments connected by a very slender thread (the second chromosome in figure 13, the X chromosome in figure 20, the third chromosome in figure 26). Because of these differences in the appearance of the chromosomes in the oögonial and the nerve-cells, oögonial divisions and nerve-cell divisions were studied in each of the translocations. The results obtained by both methods are in agreement with each other.

The chromosomes of individuals heterozygous for the translocations are shown in figures 1–19 and 21–30. All chromosomal plates contain a more or less short rod-shaped chromosome which is absent in the chromosomal plate of normal *Drosophila melanogaster*. This "new" chromosome represents, evidently, the section of the second chromosome attached to the fourth chromosome. The compound nature of this rod-shaped chromosome is in some cases marked by the presence of a constriction dividing the body of this chromosome into two parts (figures 5, 13, 15–17, 21–25, 27, 29–31). One of these parts, usually lying closer to the center of the plate than the other part, is equal in size to the free fourth chromosome present in the

Explanations of Plates 1 and 2

The drawings represent the chromosomes of flies carrying the translocations. Figures 1–12 are oögonial metaphase plates, Figures 13–32 are divisions of the neurocytes of the larval ganglia. Figures 1–15, 17–19, 21, 23–27, 29–31 contain two X chromosomes (females). Figures 16, 20, 22, 28, 32 contain one X chromosome and one Y chromosome (males). All the drawings are done at the level of the work-table, with the aid of camera lucida. The magnification is Zeiss objective 120 (1.5), and comp. oc. 30.

Plate 1

Figures 1–5, a-translocation (heterozygous), figure 6, b-translocation (heterozygous), figures 7–9, c-translocation (heterozygous), figures 10–12, d-translocation (heterozygous), figures 13–15, a-translocation (heterozygous), figures 16–18, b-translocation (heterozygous).

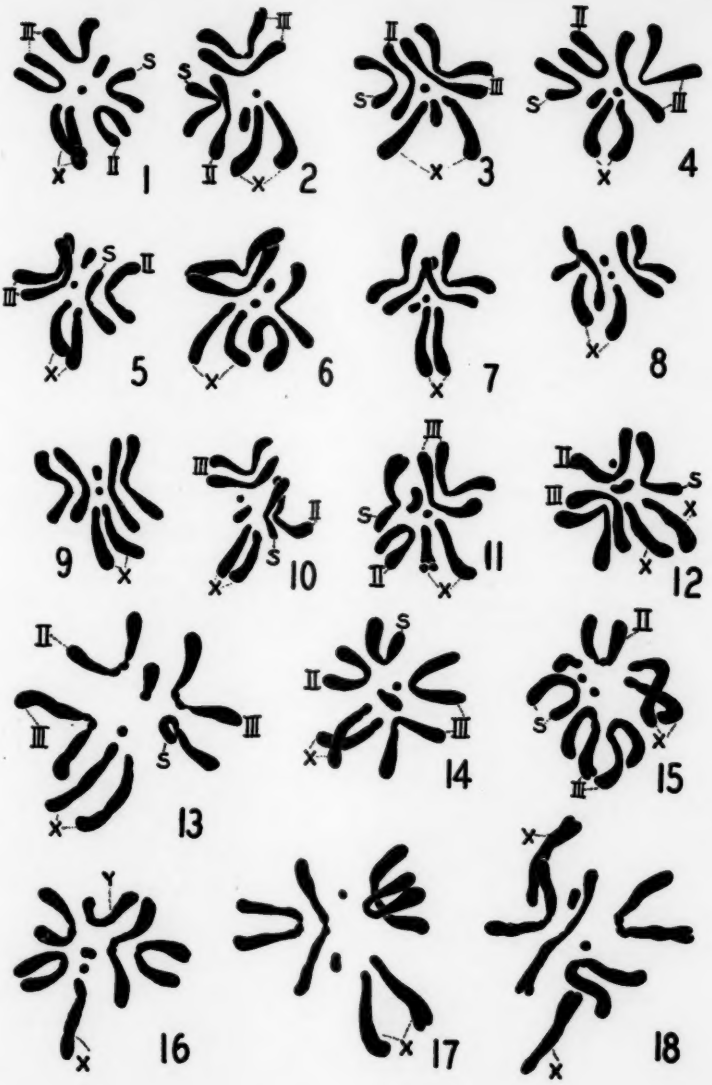
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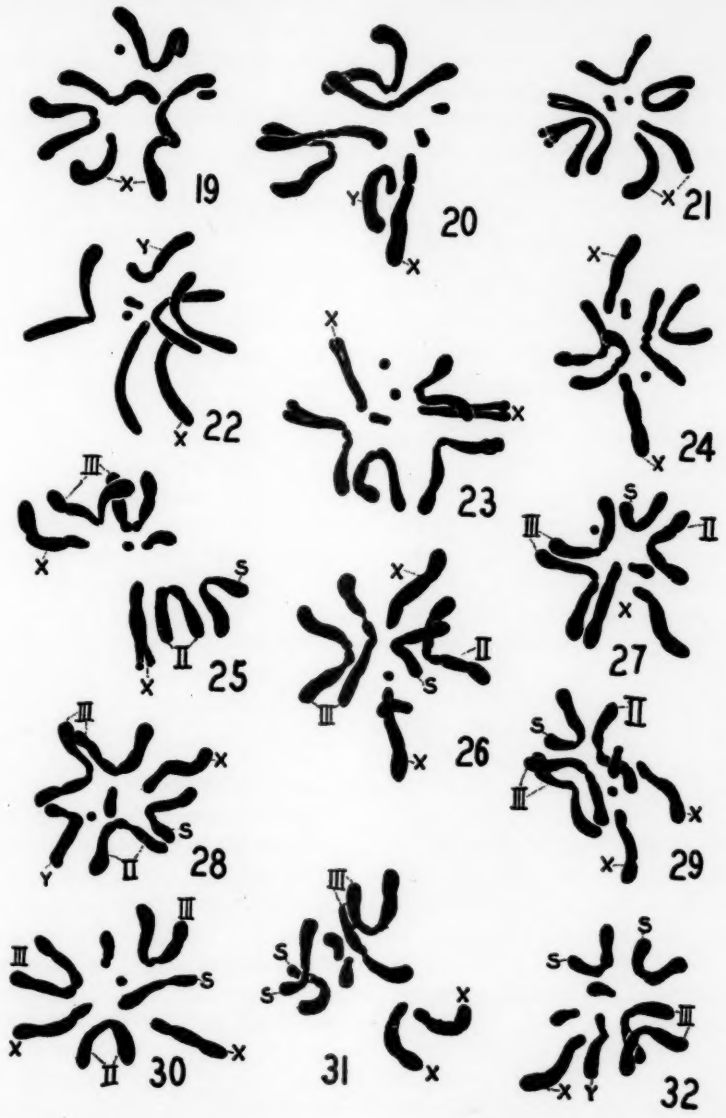
PLATE 2

FIGURE 19, b-translocation (heterozygous), figure 20, b-translocation (homozygous), figures 21–24, c-translocation (heterozygous), figures 25–30, d-translocation (heterozygous), figures 31–32, d-translocation (homozygous).

In all figures X = the X chromosome; Y = the Y chromosome; s = the second chromosome having one limb shorter than the other; II = the normal second chromosome; III = the third chromosomes. The second and the third chromosomes are marked only in those figures in which the shortening of one of the second chromosomes is clearly visible. The small round chromosomes (unmarked) are the fourth chromosomes, and the very short rod-shaped chromosomes (also unmarked) are the fourth chromosomes with a fragment of the second chromosome attached to them.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same plate. This is, probably, the fourth chromosome to which the fragment of the second chromosome is attached.

Most of the chromosomal plates studied contain only one free fourth chromosome (the small round autosome), instead of the two present in the chromosomal plates in normal flies. This is to be expected, since the other fourth chromosome is included in the "new" rod-shaped chromosome. The appearance of the few individuals possessing the "new" rod-shaped chromosome together with two free fourth chromosomes (figures 15 and 23) is due to the non-disjunction of the fourth chromosomes. This explanation was tested genetically in the III-IV translocations, which are very similar in nature to the II-IV translocations described here, and was found to be valid (DOBZHANSKY 1930a).

In a- and in d-translocation (figures 1–5, 10–15, 25–30) the pair of the shorter V-shaped autosomes consists of two partners of unequal length. One of these partners (marked in figures by the sign II) has both limbs equal in length, like the autosomes of normal flies. The other partner (marked s) has one limb shorter than the other limb. It is obvious from inspection of the figures that the difference in length between the two limbs of the unequal-armed chromosome is in most cases a little smaller than the length of the "new" rod-shaped chromosome. The unequal-armed chromosome is, evidently, the second chromosome minus a section which has been transposed onto the fourth chromosome.

In b- and in c-translocations (figures 6–9, 16–19, 21–24) no unequal-armed chromosome can be identified with certainty. This is due to the fact that the section of the second chromosome transposed onto the fourth chromosome is very short in these translocations, and its loss does not produce an appreciable shortening of the rather long second chromosome. The addition of the same section to the very small fourth chromosome is, however, visible. The longer pair of the V-shaped autosomes (III), which are the genetic third chromosomes, is normal in all plates studied in all translocations. The same holds for the two X chromosomes in females (x, figures 1–15, 17–19, 21, 23–27, 29–31), and for the X-Y pair in males (figures 16, 20, 22, 28, 32).

Individuals homozygous for translocations (figures 20, 31, 32) have two "new" rod-shaped chromosomes, and no free fourth chromosome. In homozygous d-translocation both shorter V-shaped autosomes are unequal armed (s, figures 31, 32).

The cytological evidence is, thus, in agreement with the interpretation of the genetic behavior of the translocations given in foregoing sections of this paper.

The lengths of the broken off sections of the second chromosome are both genetically and cytologically different in different translocations. In a-translocation the second chromosome is broken to the left of the locus of the gene *c* (see figure 2). The section of the second chromosome attached to the fourth contains, therefore, the genes from *c* to s_p. The length of this section equals more than 35 map-units. Since the whole right limb of the second chromosome (that is, the distance between the gene p_r and the right end of the chromosome) is about 55 map-units long, the section which is broken off in a-translocation represents in any case more than one-half of

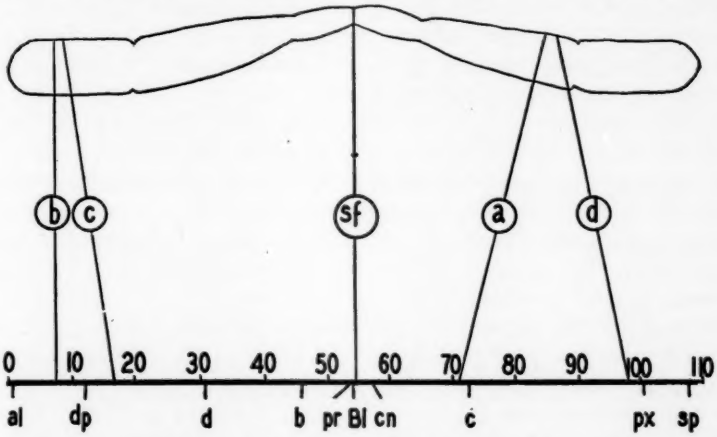

DIAGRAM 2.—The genetic and the cytological maps of the second chromosome. Letters below the line representing the genetic map of the second chromosome indicate the location of certain of the genes of the second linkage group. Letters in the circles indicate the loci of the breaks observed in translocations on the genetic and the cytological maps respectively. Sf—the spindle fibre.

the length of the limb. Cytologically, however, its length is obviously less than one-half of the length of one limb of the shorter V-shaped autosome (figures 1–5, 13–15). In d-translocation the second chromosome is broken to the left of the gene p_x. The broken-off section carries, therefore, the genes from p_x to s_p, and is much shorter than the section broken off in a-translocation. Cytologically a- and d-translocations are nearly indistinguishable, although a careful comparison shows that the rod-shaped chromosome is a little shorter in d-translocation than in a-translocation.

In both a- and d-translocation the second chromosome is broken between the subterminal constriction (which lies at about one-third of the limb-length from the end of the chromosome) and the spindle fibre, much

closer to the former than to the latter. The position of the locus of the break in respect to the subterminal constriction is very clearly visible in figure 30. The rod-shaped chromosome in this figure has two constrictions. One of these constrictions separates the fourth chromosome from the section of the second chromosome attached to it. The second constriction is probably homologous to the subterminal constriction in the normal second chromosome.

In b- and in c-translocations the second chromosome is broken to the left and to the right of the gene d_p respectively. The genetic determination of the length of the broken-off sections is very inaccurate in these translocations, due to the strong reduction of crossing over in the second chromosome. Nevertheless, one may take it for granted that in b-translocation the broken-off section is less than 13 units long, and in c-translocation its length is more than 13 but less than 30 map-units. That is to say, in c-translocation the length of the broken-off section equals at least one-fifth of the limb-length, and in b-translocation is equal to one-fifth or less than one-fifth of the limb length. Cytologically b-translocation (figures 6, 16–20) and c-translocation (figures 7–9, 21–24) are scarcely distinguishable from each other. The "new" rod-shaped chromosome in these translocations is only from twice to three times longer than the diameter of the free fourth chromosome. The length of the broken-off section of the second chromosome is, therefore, shorter than one-fifth of the length of the limb of the normal second chromosome.

A comparison of the relative genetic and cytological lengths of the sections of the second chromosomes involved in the II-IV translocations studied is presented in diagram 2. The discrepancy between the genetic and the cytological determinations of the relative lengths of these sections is so striking that the evidence derived from the study of these translocations, if taken alone, might make one doubt whether the arrangement of genes on the genetic map of the second chromosome is the same as their arrangement within the second chromosome seen under the microscope. A more complete cytological map of the second chromosome, constructed on the basis of the study of II-IV, II-Y and II-III translocations (see DOBZHANSKY 1930b), shows, however, that the sequence of genes on the genetic and the cytological maps is undoubtedly the same. The discrepancies between the genetic and the cytological maps are, as shown in the paper just referred to, due to the lower frequency of crossing over per unit of the absolute distance in the region around the spindle-fibre attachment and at the ends of the second chromosome, as compared with its frequency in the regions lying in the middle of either limb. These alternating regional dif-

ferences in the frequency of crossing over are, probably, responsible for the great genetic length of the d_p-b and c-p_z intervals which, as our data show, are very short cytologically.

A further evidence in favor of this interpretation of the discrepancies between the genetic and the cytological maps of the second chromosome was recently obtained by Doctor H. REDFIELD (unpublished). According to Doctor REDFIELD's data the map of the second chromosome constructed on the basis of a study of crossing over in triploid females is generally intermediate between the regular genetic map and the cytological map. It has been shown by REDFIELD (1930) that the map of the third chromosome of *Drosophila melanogaster* constructed on the basis of triploid crossing over is also intermediate between the genetic map and the cytological map.

SUMMARY

1. Four translocations involving the second and the fourth chromosomes were found in the progeny of males treated by X-rays. Flies heterozygous for the translocations are normal in appearance and in viability. The translocations manifest themselves by producing an apparent linkage of genes belonging to the second and to the fourth linkage groups.

2. In each of the translocations a section of the second chromosome became broken off and reattached to the fourth chromosome. In one of the translocations the breakage took place to the left of the locus of the gene c, in the second to the left of d_p, in the third to the right of d_p, and in the fourth to the left of p_z.

3. The frequency of crossing over in translocations is strongly decreased in the limb of the second chromosome in which the breakage took place, and remains normal in the opposite limb. The point dividing the two limbs of the second chromosome, which is the point of the attachment of the spindle fibre, is located near the gene p_r.

4. One of the translocations survives in homozygous form and the homozygote is normal in appearance and fertile. Two of the translocations studied seldom survive in homozygous condition, and one never survives.

5. In individuals heterozygous for translocations the section of the second chromosome attached to the fourth chromosome is distributed independently of the normal second chromosome at the reduction division. The section of the second chromosome retaining its own spindle fibre always passes to the opposite pole from the normal second chromosome.

6. One of the translocations studied produces a viable duplication. Individuals carrying the duplication have two normal second chromosomes plus a section of the second chromosome containing the locus of the gene

a_l, but not of d_p or any other genes located to the right of d_p. Such individuals are abnormal in appearance and sterile.

7. A cytological investigation of flies heterozygous for the translocations revealed the presence in their chromosomal plates of a "new" rod-shaped chromosome. This chromosome is composed of one of the fourth chromosomes with a section of the second chromosome attached. Usually only one free fourth chromosome is present in the chromosomal plates studied, and one of the shorter V-shaped autosomes has one limb shorter than the other limb.

8. In homozygous translocations two "new" rod-shaped chromosomes, two unequal-armed V-shaped autosomes, and no free fourth chromosome are found.

9. The relative lengths of the sections of the second chromosome involved in translocations were determined both genetically and cytologically. Rather striking discrepancies between these determinations are apparent.

10. These discrepancies are, presumably, due to variations in the frequency of crossing over per unit of the absolute distance in the different regions of the second chromosome.

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APPENDIX TABLES 5–8

TABLE 5

Translocation a.

$$\frac{-}{e_y} \quad \frac{1\ 2\ 3\ 4 + {}^{a}\!/_{w}\ 5\ 6\ 7}{a_1\ d_p\ b\ p_r \qquad c\ p_z\ s_p} \ \text{♀} \times e_y\ a_1 d_p\ b\ p_r\ c\ p_z\ s_p\ \text{♂}.$$

CLASSES OF THE OFFSPRING	NUMBER OBSERVED
0 Wild-type	665
0 $a_1 d_p b\ p_r c\ p_z s_p e_y$	267
Total non-crossovers	932
1 a_1	119
1 $d_p b\ p_r c\ p_z s_p e_y$	51
2 $a_1 d_p$	297
2 $b\ p_r c\ p_z s_p e_y$	222
3 $a_1 d_p b$	55
3 $p_r c\ p_z s_p e_y$	71
4 $a_1 d_p b\ p_r$	6
4 $c\ p_z s_p e_y$	7
5 $a_1 d_p b\ p_r e_y$	1
6 $a_1 d_p b\ p_r c\ e_y$	33
6 $p_z s_p$	30
7 $a_1 d_p b\ p_r c\ p_z e_y$	18
7 s_p	26
Total single crossovers	936
1, 2 d_p	6
1, 2 $a_1 b\ p_r c\ p_z s_p e_y$	8
1, 3 $d_p b$	5
1, 3 $a_1 p_r c\ p_z s_p$	3
1, 6 $a_1 p_z s_p$	5
1, 6 $d_p b\ p_r c\ e_y$	3
1, 7 $a_1 s_p$	8
1, 7 $d_p b\ p_r c\ p_z e_y$	1
2, 3 b	17
2, 3 $a_1 d_p\ p_r c\ p_z s_p e_y$	8
2, 4 $b\ p_r$	10
2, 4 $a_1 d_p c\ p_z s_p e_y$	3
2, 6 $b\ p_r c\ e_y$	4
2, 6 $a_1 d_p\ p_z s_p$	17
2, 7 $b\ p_r c\ p_z e_y$	9
2, 7 $a_1 d_p s_p$	7
3, 4 p_r	5
3, 4 $a_1 d_p b c\ p_z s_p e_y$	1
3, 7 $p_r c\ p_z e_y$	2
3, 7 $a_1 d_p b\ s_p$	2
6, 7 p_z	1
Total double crossovers	125
1, 2, 3 $d_p\ p_r c\ p_z s_p e_y$	1
1, 2, 3 $a_1 b$	1
1, 2, 4 $a_1 b\ p_r$	1
2, 3, 6 $b\ p_z s_p$	1
2, 4, 6 $b\ p_r p_z s_p$	1
2, 4, 7 $b\ p_r s_p$	1
2, 5, 6 $a_1 d_p c$	1
Total triple crossovers	7
Grand total	2000

TABLE 6
Translocation b.

$$\frac{-}{e_y} \quad \frac{1+^{a_y}2\ 3\ 4\ 5\ 6\ 7}{a_1 \qquad d_p\ b\ p_r\ c\ p_z\ s_p} \ \varphi \times e_y\, a_1 d_p b\, p_r c\, p_z s_p \sigma^{\prime}.$$

CLASSES OF THE OFFSPRING	NUMBER OBSERVED
0 Wild-type	448
0 $a_1 d_p b\ p_r c\ p_z s_p e_y$	272
Total non-crossovers	720
1 a_1	1
1 $d_p b\ p_r c\ p_z s_p e_y$	1
2 $a_1\ e_y$	1
3 $a_1 d_p e_y$	1
3 $b\ p_r c\ p_z s_p$	9
4 $a_1 d_p b\ e_y$	1
4 $p_r c\ p_z s_p$	2
5 $a_1 d_p b\ p_r e_y$	113
5 $c\ p_z s_p$	143
6 $a_1 d_p b\ p_r c\ e_y$	127
6 $p_z s_p$	240
7 $a_1 d_p b\ p_r c\ p_z e_y$	30
7 s_p	86
Total single crossovers	755

CLASSES OF THE OFFSPRING	NUMBER OBSERVED
1, 5 $d_p b\ p_r e_y$	1
3, 6 $b\ p_r c$	1
3, 4 b	1
3, 4 $a_1 d_p p_r c\ p_z s_p e_y$	1
4, 5 p_r	1
5, 6 c	21
5, 6 $a_1 d_p b\ p_r p_z s_p e_y$	10
5, 7 $c\ p_z$	4
5, 7 $a_1 d_p b\ p_r s_p e_y$	1
6, 7 p_z	3
6, 7 $a_1 d_p b\ p_r c\ s_p e_y$	2
Total double crossovers	46
4, 5, 6 $a_1 d_p b\ c\ e_y$	1
Total triple crossovers	1
Grand total	1522

TABLE 7

Translocation c.

$$\frac{-}{e_y} \quad \frac{1\ 2 + {}^{w}3\ 4\ 5\ 6\ 7}{a_1\ d_p \qquad\qquad b\ p_r\ c\ p_z\ s_p} \ \varphi \times e_y\ a_1 d_p\ b\ p_r\ c\ p_z\ s_p \sigma^{\prime}.$$

CLASSES OF THE OFFSPRING	NUMBER OBSERVED
0 Wild-type	571
0 $a_1 d_p\ b\ p_r\ c\ p_z\ s_p\ e_y$	228
Total non-crossovers	799
1 a_1	3
1 $d_p\ b\ p_r\ c\ p_z\ s_p\ e_y$	1
2 $a_1 d_p$	2
2 $b\ p_r\ c\ p_z\ s_p$	1
3 $a_1 d_p\ e_y$	59
3 $b\ p_r\ c\ p_z\ s_p\ e_y$	34
4 $a_1 d_p\ b\ e_y$	23
4 $p_r\ c\ p_z\ s_p$	35
5 $a_1 d_p\ b\ p_r\ e_y$	278
5 $c\ p_z\ s_p$	96
6 $a_1 d_p\ b\ p_r\ c\ e_y$	112
6 $p_z s_p$	385
7 $a_1 d_p\ b\ p_r\ c\ p_z\ e_y$	38
7 s_p	89
Total single crossovers	1156
1, 5 $d_p\ b\ p_r\ e_y$	1
1, 6 $a_1\ p_z\ s_p$	1
3, 4 b	5
3, 4 $a_1 d_p\ p_r\ c\ p_z\ s_p\ e_y$	1

CLASSES OF THE OFFSPRING	NUMBER OBSERVED
3, 5 $b\ p_r$	33
3, 5 $a_1 d_p\ c\ p_z\ s_p\ e_y$	6
3, 6 $b\ p_r\ c$	11
3, 6 $a_1 d_p\ p_z\ s_p\ e_y$	12
3, 7 $a_1 d_p\ s_p\ e_y$	1
4, 5 p_r	28
4, 5 $a_1 d_p\ b\ c\ p_z\ s_p\ e_y$	7
4, 6 $p_r\ c$	5
4, 6 $a_1 d_p\ b\ p_z\ s_p\ e_y$	6
5, 6 c	14
5, 6 $a_1 d_p\ b\ p_r\ p_z\ s_p$	47
5, 7 $c\ p_z$	4
5, 7 $a_1 d_p\ b\ p_r\ s_p\ e_y$	8
6, 7 p_z	11
6, 7 $a_1 d_p\ b\ p_r\ c\ s_p\ e_y$	3
Total double crossovers	204
3, 4, 5 $a_1 d_p\ p_r\ e_y$	1
3, 4, 6 $b\ p_z\ s_p$	3
3, 5, 6 $a_1 d_p\ c\ e_y$	13
3, 5, 6 $b\ p_r\ p_z\ s_p$	32
4, 5, 6 $p_r\ p_z\ s_p$	11
4, 5, 6 $a_1 d_p\ b\ c\ e_y$	10
Total triple crossovers	70
Grand total	2229

TABLE 8

Translocation d.

$$\frac{-}{e_y}\ \frac{1\ 2\ 3\ 4\ 5+^{e_y}6\ 7}{a_1\ d_p\ b\ p_r\ c\qquad p_z\ s_p}\ \varphi\times e_y\ a_1\ d_p\ b\ p_r\ c\ p_z\ s_p\sigma^{\prime}.$$

CLASSES OF THE OFFSPRING	NUMBER OBSERVED
0 Wild-type	439
0 $a_1\ d_p\ b\ p_r\ c\ p_z\ s_p\ e_y$	181
Total non-crossovers	620
1 a_1	95
1 $d_p\ b\ p_r\ c\ p_z\ s_p$	50
2 $a_1\ d_p$	207
2 $b\ p_r\ c\ p_z\ s_p\ e_y$	156
3 $a_1\ d_p\ b$	49
3 $p_r\ c\ p_z\ s_p\ e_y$	44
4 $a_1\ d_p\ b\ p_r$	33
4 $c\ p_z\ s_p\ e_y$	24
5 $a_1\ d_p\ b\ p_r\ c$	16
5 $p_z\ s_p\ e_y$	15
6 $a_1\ d_p\ b\ p_r\ c\ e_y$	1
6 $p_z\ s_p$	1
7 $a_1\ d_p\ b\ p_r\ c\ p_z\ e_y$	13
7 s_p	15
Total single crossovers	719
1, 2 $a_1\ b\ p_r\ c\ p_z\ s_p\ e_y$	7
1, 2 d_p	15
1, 3 $a_1\ p_r\ c\ p_z\ s_p\ e_y$	11
1, 3 $d_p\ b$	7
1, 4 $a_1\ c\ p_z\ s_p\ e_y$	4
1, 4 $d_p\ b\ p_r$	8
1, 5 $d_p\ b\ p_r\ c$	2
1, 6 $a_1\ p_z\ s_p$	1
1, 6 $d_p\ b\ p_r\ c\ e_y$	1
1, 7 $a_1\ s_p$	1
2, 3 b	8
2, 3 $a_1\ d_p\ p_r\ c\ p_z\ s_p\ e_y$	2
2, 4 $b\ p_r$	24
2, 4 $a_1\ d_p\ c\ p_z\ s_p\ e_y$	8
2, 5 $b\ p_r\ c$	4
2, 5 $a_1\ d_p\ p_z\ s_p\ e_y$	6
2, 6 $b\ p_r\ c\ e_y$	2
2, 6 $a_1\ d_p\ p_z\ s_p$	1
2, 7 $a_1\ d_p\ s_p$	10
2, 7 $b\ p_r\ c\ p_z\ e_y$	1
3, 4 p_r	6
3, 4 $a_1\ d_p\ b\ c\ p_z\ s_p\ e_y$	1
3, 5 $p_r\ c$	2
3, 7 $a_1\ d_p\ b\ s_p$	1
3, 6 $p_r\ c\ e_y$	1
4, 5 c	7
4, 5 $a_1\ d_p\ b\ p_r\ p_z\ s_p\ e_y$	21
4, 6 $c\ e_y$	2
4, 6 $a_1\ d_p\ b\ p_r\ p_z\ s_p$	1
Total double crossovers	165
1, 2, 3 $a_1\ b$	1
1, 2, 4 $a_1\ b\ p_r$	1
1, 2, 4 $d_p\ c\ p_z\ s_p\ e_y$	2
1, 3, 4 $a_1\ p_r$	1
1, 3, 5 $a_1\ p_r\ c$	1
1, 3, 7 $d_p\ b\ s_p$	1
1, 4, 5 $a_1\ c$	1
1, 4, 5 $d_p\ b\ p_r\ p_z\ s_p\ e_y$	4
2, 3, 4 $a_1\ d_p\ p_r$	1
2, 4, 5 $a_1\ d_p\ c$	23
2, 4, 5 $b\ p_r\ p_z\ s_p\ e_y$	35
3, 4, 5 $a_1\ d_p\ b\ c$	4
3, 4, 5 $p_r\ p_z\ s_p\ e_y$	3
Total triple crossovers	78
1, 2, 4, 5 $d_p\ c$	1
1, 2, 4, 5 $a_1\ b\ p_r\ p_z\ s_p\ e_y$	1
1, 3, 4, 5, $d_p\ b\ c$	2
Total quadruple crossovers	4
Grand total	1586

THE EFFECTS OF X-RADIATION OF LARVAE IN HABROBRACON

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The authors wish to express their gratitude to the MARINE BIOLOGICAL LABORATORY, Woods Hole, the Zoology Department of the UNIVERSITY OF PITTSBURGH, and the UNIVERSITY OF CHICAGO HOSPITAL for the use of X-ray equipment; to the Department of Zoology of the UNIVERSITY OF CHICAGO and to PENNSYLVANIA COLLEGE FOR WOMEN for use of laboratories and equipment; to the AMERICAN ASSOCIATION FOR THE ADVANCEMENT OF SCIENCE for the grant to the senior author, and to the Committee on X-rays of the NATIONAL RESEARCH COUNCIL whose grant to P. W. WHITING has been of help indirectly in the way of furnishing a general assistant for keeping stocks and breeding host caterpillars. The drawings represent the careful and painstaking work of Miss KATHRYN A. GILMORE.

INTRODUCTION

Treatment of larvae of the parasitic wasp, *Habrobracon juglandis*, by X-rays, was begun in January, 1929. Progeny from crosses of different stocks were used with pure stocks sometimes treated as checks. Females resulting from crosses are heterozygous and diploid; males are haploid and resemble their mothers. Heterozygous larvae, females, were treated in order that the destruction of any chromosome or part of a chromosome bearing a dominant allelomorph might be recognized by the somatic appearance of the recessive character which would appear as a spot. The

animal possessing it would be a mosaic. The somatic mutation of a dominant allelomorph in a larval cell to the recessive would produce the same effect. A somatic mutation, dominant or recessive, in any locus in a larval cell of a male might result in mosaicism because of haploidy of the males.

The progeny of treated females were carefully studied for anomalous individuals. Germinal mutations would be expected to appear among the haploid sons of these females. Such mutations would appear in daughters, (1) if these mutations were dominant, (2) if the same mutation had occurred in the gonads of both parents during their treatment as larvae, (3) if a recessive mutation occurred and its dominant allelomorph had been destroyed. Since dominant mutations are rare the first possibility would be unlikely. The second and third conditions would be highly improbable. It seemed quite evident then that no mutations would appear among the daughters of treated females and this supposition has been borne out by results.

Larvae heterozygous for reduced wings and ivory eyes (*RrOo*^{i}) were used because of the fact that individuals with mosaic eyes, or two kinds of wings, or both, occasionally appear among the sons of such females and there was the possibility that X-ray treatment would affect their rate of occurrence. This mosaicism is without doubt due to binuclearity of the egg (WHITING 1928), and, in the case of the eye, is almost always associated with apparent mutation of ivory to orange.

No controls were run during the preliminary experiments and numbers are small. For these reasons the results will be summarized briefly. In the last experiment (7) careful brother-sister controls were run and numbers are sufficiently large to make results worthy of more detailed study.

TECHNIQUE

Mated females were placed in shell vials with host caterpillars. These females were transferred at the same hour every day and on the fourth day the parasitized hosts were transferred to gelatine capsules and treated. Each capsule contained larvae within twenty-four hours of the same age and from several parents of the same genetic constitution. This daily transferring with treatment every fourth day was continued during the lives of the mothers. After some experience it was found that one and two day larvae resembled each other in their responses while three and four day larvae were likewise similar to each other. Females were, therefore, transferred every second day and the larvae treated every fourth day in the later experiments. Controls were also transferred to capsules so that any abnormalities which might be due to injury from handling would tend to

be the same in both groups. All larvae were left in capsules to complete development. Except during time of treatment cultures were kept in an incubator at 30°C. Coolidge tube with tungsten target was used throughout. A Victoreen Dosimeter, supplied by the Committee on X-rays of the NATIONAL RESEARCH COUNCIL, served for accurately measuring treatments. An aluminum shield was used after preliminary experiments demonstrated that larvae were all killed by short treatments without a shield, this probably due to heat effects.

EXPERIMENTAL DATA

Experiment 1

Virgin females from the oldest and best known type stock, number 1, (plate 1, figure 3) were crossed to males with ivory (o^i) eyes and reduced (r) wings (figures 1 and 2) from stock number 27, likewise an old and well tested stock. Progeny from these matings were handled as described above. Conditions of treatment were filter, 1 mm aluminum; peak voltage, 50 K. V.; milliamperes, 5; distance, 15 cm; durations, 10, 15, 20, 40, and 60 minutes. In roentgen units this represents a range of from about 730 to 4378. These dosages were selected more or less haphazardly since there were no means of knowing which would be best.

In all, 255 adults emerged, 75 in four day group, 55 in three, 102 in two, and 23 in one. In many of the capsules, especially those given higher treatments at four days of age, there was found a high percentage of dead animals still within cocoons (66.66 ± 0.99 for four day group, 28.57 ± 5.15 for three, 28.67 ± 3.78 for two, and 26.08 ± 9.16 for one day). (Standard errors rather than probable errors are used following percentages in this paper.) These numbers represent fewer than had actually died for they were not carefully counted in all cases and could not all be counted in younger groups where the majority died almost immediately after treatment. The fact that treatment sometimes had a delayed effect is of some interest. Treated larvae would often spin cocoons, pupate, and metamorphose, but appeared to be too weak to go through the task of emerging. If cocoons were opened with a needle wasps would sometimes crawl out and die within a short time. They were occasionally found dead with heads and prolegs projecting from cocoons.

Numbers for any one dose and age group are too small to be significant but indications are that 10 and 15 minute treatments had little effect on any group while 20 minutes, although not affecting older groups, killed all one-day larvae. Treatments of 40 and 60 minutes showed decided lethal effects on two older groups and killed all but one larva in the two younger

DESCRIPTION OF PLATE 1

FIGURES 1–12.—×13.3.

FIGURES 13–17.—×21.6.

Normal wings.

FIGURE 1.—Reduced primary and secondary wings.

FIGURE 2.—Extreme reduced primary wings, left and right.

FIGURE 3.—Type primary and secondary wings.

Right and left primary wings of treated individuals showing shot.

FIGURE 4.—Type (*RR*) No. 31 female. Treatment 3250 r units.

FIGURE 5.—Type (*RR*) No. 1 female. Treatment 3250 r units.

FIGURE 6.—Type (*R*) No. 1 male. Treatment 3250 r units.

FIGURE 7.—Heterozygous (*Rr*) female (No. 27×No. 1). Treatment 3250 r units.

FIGURE 8.—Patroclinous (*Rr*?) male. (No. 27×No. 1). Treatment 3250 r units.

FIGURE 9.—Heterozygous (*Rr*) female (No. 27×No. 31). Treatment 1950 r units.

FIGURE 10.—Heterozygous (*Rr*) female (No. 27×No. 31). Treatment 2600 r units.

FIGURE 11.—Heterozygous (*Rr*) female (No. 27×No. 31). Treatment 3250 r units.

FIGURE 12.—Heterozygous (*Rr*) female (No. 27×No. 31). Treatment 3900 r units.

Type and "Pronotum."

FIGURE 13.—Side view, head and prothorax, normal male.

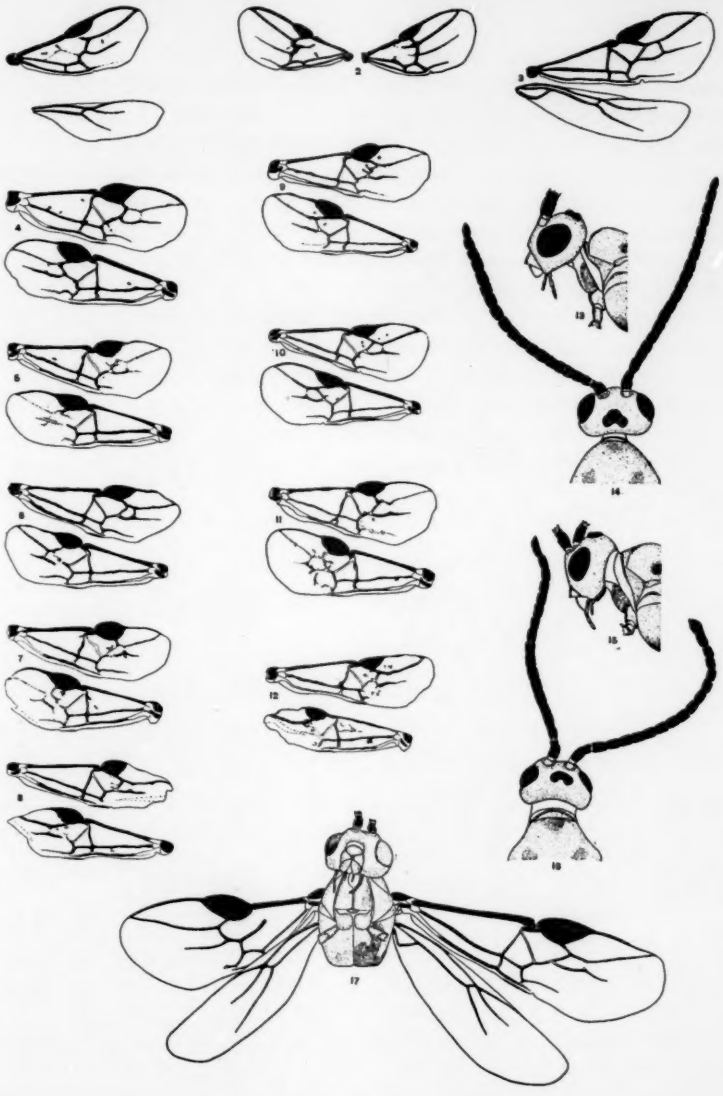
FIGURE 14.—Dorsal view, head and neck, normal male.

FIGURE 15.—Side view, head and prothorax, "pronotum."

FIGURE 16.—Dorsal view, head and neck, "pronotum."

Mosaic.

FIGURE 17.—Ventral view, head and thorax. Right eye type and orange, left eye ivory; right wing reduced, left type; right mesosternum light, left dark.



groups. Among 75 adults emerging from treated four-day larvae 9 or 12.0 $\pm$3.7 percent were abnormal in appearance, among 55 in three-day group 23 or 41.82$\pm$6.65 percent, among 102 in two-day group, 10 or 9.80$\pm$2.94 percent, and among 23 in one-day group 5 or 21.74$\pm$8.60 percent.

The freaks can be classified as follows; 16 with wings wrinkled and wing veins more or less disorganized, 19 with antennal segments fused or abnormal, 1 with antennae abnormal and wings wrinkled, 1 with abnormal abdominal sclerites, 1 with abnormal abdomen and wrinkled wings, 2 with abnormal genitalia, 5 with feet and antennae abnormal, 1 with legs and antennae deformed, median ocellus small and sting abnormal, and 1 resembling the last but with normal sting. Those with wing veins disorganized resembled reduced in that respect. Wing shape and size and fundamental vein pattern were all similar to type. The disorganization was therefore interpreted as due to some physiological change rather than to chromosome alteration (figures 4–12). No ivory patches were found in the eyes of the females. None of the abnormal types capable of reproduction transmitted defects to progeny.

TABLE 1

Breeding tests of treated females in experiment 1.

DOSE IN r UNITS	AGE OF TREATED LARVAE DAYS	♀♀ SET	PERCENT DYING WITHOUT PROGENY	TOTAL PROGENY	PROGENY PER FERTILE ♀	MOSAICS	MUTATIONS	FREAKS
730	2	9	22.22	171	24.43	0	0	0
	1	11	53.64	111	22.50	0	0	0
1095	2	3	0	35	11.66	0	0	0
	1	1	100.	0	0	0	0	0
1460	4	12	50.	280	46.66	0	1	2
	3	8	50.	122	30.50	0	0	0
	2	7	85.71	18	18	0	0	0
2919	4	3	100.	0	0	0	0	0
	3	17	88.23	81	40.50	0	0	0
4378	4	4	100.	0	0	0	0	0
	3	10	90.	1	1	0	0	0
Totals		85	65.88	819	28.24	0	1	2

Eighty-five treated females were set with results summarized in table 1. A high percentage, 65.88$\pm$5.14, died without progeny. This was not due

entirely to sterilization but to weakness resulting in early death. Many treated animals die soon after emergence.

Average number of progeny per fertile female is small for all groups but especially for those where females had been treated as one and two day larvae.

Two abnormal males appeared among the offspring of the fertile females. One had very small eyes and was possibly a mutant but is not classed as such since he had no progeny. The other had a double right primary wing. He was not bred. Another fraternity contained among 84 sons 2 with yellow basal antennal segments. The mother had been treated 20 minutes as a four-day larva (1460 r units). This character proved to be one of the four dominant mutations found to date. Mutation rate in experiment 1 is therefore 1 in 728 males (0.14 ± 0.14). No mosaics appeared.

Experiment 2

Experiment 2 was carried on at Woods Hole during July and August, 1929. The conditions of treatment were somewhat uncertain and the individuals treated a miscellaneous group. The data (table 2) therefore are

TABLE 2

Summary of individuals directly treated in experiment 2.

DURATION (MINUTES)	35					50				
SEX	♂♂		♀♀		♂♂ and ♀♀	♂♂		♀♀		♂♂ and ♀♀
AGE OF TREATED LARVAE (days)	NORMAL	FREAKS	NORMAL	FREAKS	DEAD COUNTED	NORMAL	FREAKS	NORMAL	FREAKS	DEAD COUNTED
1	50	1	16	1	47	0	0	0	0	0
2	123	4	112	0	298	0	0	0	0	30+
3	132	2	110	6	237	3	0	5	3	95+
4	244	22	202	9	100	19	4	35	5	59+
Totals	549	29	440	16	682	22	4	40	8	184+

not of great significance in any respect except that they do corroborate in a general way the results obtained in experiment 1. A recessive mutation, beaded, appeared in first generation from treated. Treatments were as follows (in so far as they could be ascertained); filter, 1.32 mm aluminum; peak voltage, 65 K. V.; milliamperes, 6; distance, 16.5 cm; durations, 35 and 50 minutes. No attempt was made to express these treatments in roentgen units since no dosimeter was available for measurements.

Percentages of freaks are again high, 4.35 ± 0.63 for 35 minute treatment, 16.22 ± 4.28 for 50 minute treatment. The difference between these percentages is 11.87 ± 4.33. Percentage found dead in capsules in 35 minute group is 39.74 ± 1.18, in 50 minute group, 71.32 ± 2.82, difference 31.58 ± 3.05. No mosaics of eye color or wing character were found. Occasional broken veins, as described above, were noted. As was the case in experiment 1 the females producing no progeny were not simply sterilized but had so little "vitality" that they died within a few hours after being set with caterpillars (table 3). They were usually normal in appearance in every way. Most females living beyond the first day after emergence produced some offspring, occasionally a fair number.

TABLE 3

Breeding tests of treated females in experiment 2.

DURATION (MINUTES)	♀♀ SET	PERCENT DYING WITHOUT PROGENY	TOTAL PROGENY	PROGENY PER FERTILE ♀	MOSAICS	MUTATIONS	FREAKS
35	222	67.57	926	12.86	1	1	13
50	25	52.00	147	12.25	0	0	0

Females in this experiment had been set, two or three in each vial. If more than two individuals were produced all the females in the vial were considered to have reproduced so that numbers recorded as dying without progeny represent a minimum. In 35 minute group 67.57 ± 3.14 percent died without progeny, in 50 minute group 52.06 ± 9.99. Difference is 15.57 ± 10.47.

Among 1073 offspring counted 13 non-inherited abnormalities appeared, 1.21 ± 0.33. This is considerably higher than expected in untreated stocks. There were 11 with abnormal abdominal sclerites, 1 with notched wings, and 1 with very broad abdomen. Individuals having abnormal sclerites were selected and tested and the character reappeared irregularly among descendants indicating possible hereditary tendency of the stock.

One mosaic (346) was found among the 161 sons of females heterozygous for ivory (0.62 ± 0.62 percent). In all other cases when an eye mosaic has been produced by a type female carrying ivory, all or most of the non-type facets have been orange. This male had an ivory right eye, ivory and black left, ivory ocelli, type right wing, and reduced left. It was tested by crossing to ivory and ivory reduced females. With five it gave ivory daughters, with one, 2 ivory reduced daughters. Gonads were therefore mosaic. There have been a few cases (WHITING 1928) where males have produced two types of daughters. Ratios and time of appearance of the different

types have indicated mosaicism of gonads rather than heterozygosis (WHITING and WHITING 1927).

The single mutation, beaded, first became evident among the sons of a heterozygous female which had been treated 35 minutes as a larva. There were 19 mutants and 8 non-beaded males in the fraternity. Many of the mutant males were feeble but a few matings were secured and beaded was found to be inherited as a recessive, female-sterile form.

Forty-three granddaughters of treated females were tested. Of these 13 (30.23 ± 7.0 percent) produced no progeny. The thirty fertile females produced in all 872 normal offspring, 29.06 offspring per fertile female, an average much smaller than any in subsequent controls studied.

Experiments 3, 4, 5, and 6

Results of experiments 3, 4, 5, and 6 are summarized in tables 4 and 5. Almost all larvae were from number 27 females by number 31 males. A few

TABLE 4

Summary of individuals directly treated in experiments 3, 4, 5, and 6.

EXPERIMENT NUMBER	DOSE IN r UNITS	TREATED		CONTROLS	
		♂♂	♀♀	♂♂	♀♀
3	1824	283	547	..	..
4	3977	15	57	188	194
5	2280	203	306	248	369
6	2183	4	20	5	42
Totals		505	930	441	605

were from pure number 31. Controls are brothers and sisters of treated. All treatments were done with peak voltage, 50 K. V.; milliamperes, 8; distance, 15 cm; experiment 3 with filter, 1 mm aluminum; duration 25 minutes: experiment 4 with filter, $\frac{1}{2}$ mm aluminum; duration, 30 minutes: experiment 5 with filter, $\frac{1}{2}$ mm aluminum; duration, 20 minutes: experiment 6 with filter, $\frac{1}{2}$ mm aluminum; duration, 25 minutes. Since nothing new would be brought out by summarizing according to age at time of treatment different groups have been added together. Dashes indicate that no tests were made.

In these experiments no detailed records were kept of defective and dead individuals among treated since nothing new in principle would be established by taking time for recording so many abnormalities. Any new or symmetrical defect was recorded and tested and every individual was studied for mosaicism in eyes and wings. One female was found that had

but one-half a head. One antenna, all ocelli, and one eye were absent as well as all tissue normally surrounding these. There remained mouth parts, one eye, and one antenna with very little other tissue. She fed on honey but did not produce offspring. One male with very thick antennae was sterile. One female had a double foot. A number showed disorganized veins but no very careful records were taken of these except in experiment 5. Results of this will be included in summary of experiment 7.

Table 5 summarizes results of tests of 217 females treated as larvae and of 70 sisters run as controls. Of treated, 32.72 ± 3.18 percent died almost as

TABLE 5

Breeding tests of treated females in experiments 3, 4, 5, and 6.

EXPERIMENT NUMBER	DOSAGE IN r UNITS	♀♀ SET	PERCENT DYING WITHOUT PROGENY	TOTAL PROGENY	PROGENY PER FERTILE ♀	MOSAICS	MUTATIONS	FREAKS
3 treated	1824	117	11.11	*1087+	*10.49+	0	0	3
controls		..	..	..	..	..	..	..
4 treated	3977	54	87.04	73	10.43	0	0	0
controls		41	17.07	3614	106.29	0	0	17
5 treated	2280	35	31.43	1589	66.21	3	0	3
controls		29	3.45	3127	111.67	1	0	1
6 treated	2183	11	0	1023	93.0	0	0	0
controls		..	..	..	..	..	..	..
Totals treated		217	32.72	3772	25.83	3	0	6
controls		70	11.43	6741	108.72	1	0	18

* Fertile females in experiment 3 were not fully tested. Numbers of progeny are, therefore, not comparable with those in other experiments.

soon as set and produced no offspring. The remainder averaged 25.84 progeny each, 3772 in all. Of controls, 11.43 ± 3.80 percent died and produced no progeny. The remainder averaged 108.72 progeny each, 6741 in all. Percentage dying without progeny varies directly and average number of offspring per fertile female varies inversely as the number of roentgen units of treatment.

Of the three mosaics from treated diheterozygous females one (379) had type eyes, the right wing type, the left reduced. This bred like an ivory reduced indicating still greater mosaicism since eyes were type and gonads bearing ivory. The second (383) had right eye orange, left black and orange, ocelli light, right wing type, left reduced. This was not tested. The third (405) had orange eyes. Since it bred as type producing 166 type daughters

it was a mosaic. Orange eye color possibly represents a somatic mutation from ivory. Reasons for not including this among mutations will be considered later.

The single mosaic found in a control culture had ivory eyes and mosaic wings. It bred as ivory non-reduced.

The six freaks found in cultures from treated were 1 with short primary wing, 1 with "tumor" on eye, 1 very small in size and resembling a mutant stock, miniature, 1 with wrinkled wings, and 2 with one eye missing. Of those produced by control females 17 had wrinkled wings, 1 abnormal abdomen.

No mutations were produced in either treated or controls among 3768 males in former and 6345 males in latter group.

Experiment 7

Since numbers are not especially large in these earlier experiments, controls not used in all cases and treatment somewhat uncertain in some, it was planned to undertake a large experiment where all treatments could be given on the same machine and under carefully controlled conditions. This plan was carried out at the UNIVERSITY OF CHICAGO during the summer of 1930. Large numbers of virgin females were isolated by the capsule method. In this method larvae are spread out on paper in petri dishes. When they have pupated each is separated by cutting the paper and placed in a gelatine capsule. Ivory reduced, number 27, females were used, as before, and they were crossed to type males from number 31. Pure stock number 31 (treated and controls) were also used as controls on the wing disorganization. There were no complications due to disease which in the past has sometimes given trouble. Two females were placed in each vial with two host meal worms. Every other day the females were transferred and given two fresh caterpillars. The parasitized caterpillars, covered with young larvae, were separated and each placed in a separate gelatine capsule. If one caterpillar had been given to one female the progeny could not be separated and if two had been given to one female she would not have parasitized them sufficiently by the second day. Since a female oviposits on any stung caterpillar and does not confine her attentions to one, each caterpillar without any doubt contained progeny from both females.

Plans were made to treat these progeny under the usual conditions but upon consultation at the UNIVERSITY OF CHICAGO HOSPITAL where the X-raying was done it was found that these would have to be altered. Peak voltage used was 60 K. V.; milliamperes, 5; filter, ½ mm aluminum; distance, 15 cm; and durations, 24, 32, 40, and 48 minutes, which, expressed

in roentgen units, correspond to 1950, 2600, 3250, and 3900, respectively.

All individuals were kept in an incubator at 30°C except during time of irradiation when both groups were removed and controls handled exactly like treated. Raying was done every fourth day. Individuals treated as three and four-day larvae are designated series a, those as one and two-day larvae, series b. As soon as females, treated as larvae, emerged they were set with caterpillars. Twelve matings were planned from each group, ninety-six in all, but from some groups there emerged less than twelve females and in other cases more than twelve were set due to high mortality. The females were virgin for the most part since they were collected promptly and usually emerged earlier than the males. Females from both a and b series treated 40 and 48 minutes were usually given caterpillars first stung by untreated females in an attempt to get at least a few eggs without requiring the feeble females to undergo the exertion of stinging the caterpillars.

TABLE 6

Comparative susceptibility to treatment of 1–48 hour larvae (b series) and 49–96 hour larvae (a series) in experiment 7.

DOSE IN r UNITS	SERIES	TREATED		CONTROLS	
		TOTAL	PERCENT b	TOTAL	PERCENT b
1950	a	604		497	
	b	236	28.09	337	40.41
2600	a	121		227	
	b	29	19.33	128	36.06
3250	a	287		514	
	b	39	11.96	417	44.79
3900	a	144		382	
	b	9	5.88	434	53.19

For summaries in tables 6 and 9, number 27 by number 31 and pure number 31 are combined since they showed no important differences. A significant study of the relative effects of treatment on series a and series b (49–96 hour and 1–48 hour larvae) can be made in this experiment for careful controls are available. With no transferring of larvae and eggs from vials to capsules we would expect approximately the same numbers to emerge from series a and b. As a result of the transfer we would expect fewer progeny in b series because of the loss of some eggs and very young larvae. Eggs are scattered on surface of host and are easily lost. This can

be observed in table 6 where series b under Controls is smaller than series a in every case except the last. The difference represents loss of eggs and young larvae through being shaken from host. Under Treated it can be seen that percent b, $b \times 100/a+b$, is much smaller in every case than in controls and that this difference increases with length of treatment. These differences are highly significant and especially so in view of the fact that the progeny in each control and treated series are from the same females.

The possibility that haploid males might be more susceptible to treatment than diploid females had been considered. Any lethal arising from injury or change in a chromosome would not have the normal allelomorph to counterbalance the injurious effect in the males. Data were therefore summarized with this in mind. Among total treated numbering 1470 there were 551 males or 37.48 ± 1.26 percent. Among 2936 controls 1653 or 56.30 ± 0.91 percent were males. The difference between these percentages is 18.82 ± 1.56. Sex ratio is an uncertain question in Hymenoptera and one about which one cannot draw any definite conclusions except where offspring from the same mothers produced at the same time are involved, as is the case here. We can conclude then that haploid males are significantly more susceptible to treatment than their diploid sisters.

A careful record of physical abnormalities in directly treated and controls was not kept. However, all individuals were studied for mosaic eyes and wings. No mosaic eyes were found. A high percentage of individuals appeared having wing veins disorganized and resembling reduced to some extent. This had been noted in previous experiments and it was now decided to make a detailed study of the character and combine results with those found in experiment 5. Accordingly all animals were examined and those not set were preserved in alcohol for future study. Figures 4–12 show disorganized or "shot" wings in different stocks and under different treatments. The animals in each group were carefully studied and wings showing greatest degree of disorganization were selected in each case for drawing. The wings drawn are exceptional in figures 4, 5, and 6, since homozygous (*RR*) and male (*R*) wings but rarely showed so high a degree of shot. In figures 7–12 the wings are typical of the shot condition found in heterozygous (*Rr*) wings.

A summary of this later study of preserved specimens appears in table 7. No disorganization was found in controls. It may be noted that from the cross of number 27 females by number 31 males the percentage of shot is high in series a and increases with length of treatment up to 3250 r units, then decreases. In series b it is low or 0. Males are not recorded here for they were of the reduced type and shot normally as shown in figures 1 and

2. From type stock number 31 it appears that percentage of shot is very low in both sexes. The difference between heterozygous (*Rr*) females and homozygous (*RR*) females is still greater than indicated by this table for the degree of disorganization is great in the former and very slight in the latter. As mentioned above the drawings of *RR* and *R* wings are the ex-

TABLE 7

Wing venation of individuals treated as larvae in experiments 5 and 7.

DOSE IN F UNITS	SERIES	NUMBER 27 ♀♀ × NUMBER 31 ♂♂			NUMBER 31					
		Rr			*RR*			*R*		
		+♀♀	SHOT ♀♀	PERCENT SHOT	+♀♀	SHOT ♀♀	PERCENT SHOT	+♂♂	SHOT ♂♂	PERCENT SHOT
1950	a	188	24	11.32	188	1	0.53	209	1	0.48
	b	65	1	1.51	83	0		70	0	
2600	a	56	8	12.5	39	0		69	1	1.43
	b	6	0		15	0		9	0	
3250	a	74	33	30.84	58	4	6.45	83	3	3.49
	b	17	0		6	0		0	0	
3900	a	47	15	24.19	45	0		33	1	2.94
	b	0	0		4	0		0	0	

ceptional extremely shot, those of *Rr* wings more nearly typical. In most of the shot heterozygous females the veins are badly disorganized and quite different from type whereas in treated type individuals there was usually merely a slight break or a small additional "island" of vein. By comparing figures 9, 10, 11, and 12, primary wings of heterozygous (*Rr*) females treated 1950, 2600, 3250, and 3900 r units respectively, it can be observed that degree of shot increases with increase in dosage.

These data indicate that the presence of recessive factor reduced in heterozygous condition is largely responsible for the more extreme types of shot. Another fact to be noted is that the treatment of the younger larvae (series b) produces shot but rarely. Fifty-four heterozygous females treated with 2600 r units as five day larvae showed no shot. All evidence points to the third or fourth day of larval life as the time when treatment is most effective in this respect.

Since high percentage and degree of shot was found to be correlated with the heterozygous condition it was decided to make some crosses which would result in patroclinous males and see whether they would resemble

their diploid sisters in their response to treatment. Accordingly crosses were made between virgin females from number 27 and type males from stock number 1. Stock number 1 larvae were treated as controls. Results appear in table 8. Treatment with 3250 r units was selected since this had

TABLE 8

Wing venation of individuals treated as larvae (series a, dose 3249 r units) in experiment 7.

NUMBER 27 ♀♀ × NUMBER 1 ♂♂						NUMBER 1					
Rr			*Rr*?			*RR*			*R*		
+♀♀	SHOT ♀♀	PERCENT SHOT	+♂♂	SHOT ♂♂	PERCENT SHOT	+♀♀	SHOT ♀♀	PERCENT SHOT	+♂♂	SHOT ♂♂	PERCENT SHOT
492	230	31.85	34	16	32.0	53	18	25.35	35	7	16.66

consistently produced the highest percentage of shot in the preceding experiment. An unexpected result occurred, for type number 1 showed a high percentage of the shot condition. Here again, however, as in stock number 31, the degree of shot was slight. The type, supposedly diploid, (*Rr*) males (figures 8) showed both percentage and degree similar to their diploid (*Rr*) sisters. Their extreme disorganization gives an additional argument for their diploidy.

Reference to table 9 will make clear the effects of various treatments on females in respect to their mortality and sterility. It will be seen that per-

TABLE 9

Breeding tests of treated females in experiment 7.

DOSE IN r UNITS	SERIES	TREATED				CONTROLS			
		♀♀ SET	PERCENT DYING WITHOUT PROGENY	TOTAL PROGENY	PROGENY PER FERTILE ♀	♀♀ SET	PERCENT DYING WITHOUT PROGENY	TOTAL PROGENY	PROGENY PER FERTILE ♀
1950	a	33	36.36	1653	78.71	24	8.33	2330	105.90
	b	36	58.33	551	36.73	19	15.79	1837	114.81
2600	a	18	33.33	815	67.92	17	5.88	2394	149.37
	b	13	76.92	24	8.0	2	50.0	54	54
3250	a	43	83.72	179	24.44	24	4.17	2891	125.69
	b	10	60.0	399	99.99	8	0.	1071	133.87
3900	a	29	58.62	327	27.25	25	8.00	2946	128.08
	b	..	..	..	..	..	..	..	..
Totals		182	59.34	3940	53.24	119	8.40	13523	124.02

centage of females set that died without progeny is high in all treated groups and that this percentage rises decidedly for series b in first two groups where numbers are large enough to be significant. Lower percentages for those treated with 3250 r units, series b, and with 3900 r units, series a, may be explained by the fact that the females in these groups were fed stung caterpillars. Series b females treated wtih 3900 r units were not strong enough to set.

Average number of progeny per fertile female tends to be greater for series a. The single exception to this, 3250 r treatment, in number 27 by number 31 represents progeny of four females only, one giving 187 offspring, one 8, one 153 and one 51. In all cases average progeny per treated female is considerably smaller than per control.

TABLE 10

Rate of production of mutations, mosaics, and non-heritable abnormalities by treated and control females in experiment 7.

		TOTAL	FREAKS	PERCENT FREAKS	TOTAL ♂♂	MOSAICS	PERCENT MOSAICS	MUTATIONS	PERCENT MUTATIONS
Number 27 × Number 31	Treated	2709	3	0.11	2682	5	0.19	2	0.07
	Controls	8840	3	0.03	8741	6	0.07	1	0.11
Number 31	Treated	1231	4	0.32	1217	0	0	0	0
	Controls	4683	8	0.17	3733	0	0	0	0

Treated and control females were set as soon as emerged, fed healthy caterpillars, and transferred according to the usual technique, every attempt being made to get as many offspring as possible from each female. Offspring were carefully studied, controls as well as treated. Every abnormal individual capable of reproduction was tested as were mosaics. In all, 301 females were set of which 183 produced 17,463 progeny.

The freaks numbered 7 in treated and 11 in controls. The former group consisted of 1 with wrinkled wings, 1 with one eye only, 1 with abnormal abdomen, 1 with antennae twisted, 1 with antennal segments fused, 1 with extra wing, 1 with bar eyes, clubbed antennae and a well developed "collar" or pronotum pictured in figures 15 and 16 (compare with type, figures 13 and 14). Among the controls were found males, 1 with abnormal genitalia and antennae, 4 with wrinkled wings, 1 with antennae bent, 1 with one eye small, 1 with four ocelli, 1 with abnormal venation; and 2 females, each with one primary wing small in size but with normal venation. The

male with pronotum and bar eyes was symmetrical and gave every indication of being a mutant but the character did not reappear among a large number of F_2 males counted. It is of some interest that both abnormal females showed the same unusual characteristic, one short wing, possibly a haploid structure.

Mutations or inherited abnormalities would be expected in sons only, except for dominants. Among 12,474 control males there appeared one mutation, "confluent." A single confluent male appeared in a fraternity of 195 males. The character has proved to be recessive, female-sterile, and variable in its expression depending upon temperature. Among 3899 sons of treated were found two mutants, "stumpy" and "truncate." The former was produced by a heterozygous female in series b exposed to 3250 r units, the latter by a heterozygous female in series a exposed to 2600 r units. Stumpy appeared in 1 male among 186 brothers, truncate in 1 male among 70 brothers. Both are recessive; stumpy breeds true, truncate is uncertain in appearance. Difference between percentages of mutations in the two groups is not statistically significant.

Mosiacs, other than sex mosaics, apeared only among progeny of heterozygous females as was expected. In all, eleven mosaics were found, five among 2682 sons of treated females and six among 8741 sons of controls. Sex mosaics would not be expected since they develop only from fertilized eggs and most of the females tested had not mated.

Mosaics may be classified into two groups, (1) those with eyes mosaic for black and orange, or ivory, or wings mosaic for type and reduced, or both; and (2) those with both eyes orange. The second group may be subdivided into (a) those breeding as genetic constitution of mother would lead one to expect and (b) those breeding as orange. The last type (b) is really not a mosaic but a mutation. Its inclusion in this group will be explained later. An example of (a) has been described under experiments 3–6. Descriptions of three others follow.

Mosaic 418 is a male with left eye type, right orange, ocelli and wings type. It was tested by mating to four ivory reduced females and produced in all 30 type daughters. It should be recalled at this point that the type mother was heterozygous for ivory, and that orange, a third allelomorph of ivory and type, was not present in parent.

Mosaic 417 had type eyes, the right wing reduced, the left type. When crossed to three ivory reduced females it produced 27 daughters, all type.

Male 419 and others like it have led us to believe that the orange appearing in mosaics from type-ivory females is really a mutation, for this individual had orange eyes and bred as orange. When crossed to ivory re-

duced females it gave 24 orange daughters. They bred like regular orange stock.

In the 11 mosaics included in this experiment 3 had eyes mixed in color, 2 had two types of wings, 3 were mosaics for both eye and wing characters, 1 was orange breeding as orange, and 2 were orange and not tested. Figure 17 shows ventral view of one of these mosaics (422). Right eye is type and orange, left eye ivory, right primary wing reduced, left type, and the mesosternal difference in color brings out a previously unnoticed genetic difference between the two parent stocks.

A note should be added here including data from a short experiment mentioned above. Five day larvae from crosses of number 27 females by number 31 males were treated with 2600 r units, conditions as in experiment 7. There emerged 54 females and 19 males. Twelve females were set of which two died without producing offspring. The remaining ten produced in all 576 males. Two of these were mosaic and one a mutant, "kidney" eyes. Percentage of anomalous types is unusually high and suggests that five days may be a good age for treatment if changes are desired in progeny.

Summarizing counts of progeny of irradiated and control females in all experiments there were found 11 mosaics, 5 mutations, and 28 freaks among 10,224 offspring of irradiated; 7 mosaics, 1 mutation, and 29 freaks among 20,301 offspring of controls.

DISCUSSION

The classification of anomalous individuals into mosaics, mutants, and freaks will perhaps require some explanation. The term mutant is limited in this paper to any animal showing a new character and transmitting it to its offspring, the term mutation limited to a genic change. Occasionally a somatic character resembling an unquestioned mutant character has appeared. Since the mutant nature of these cases is doubtful in Habrobracon they are not classed as somatic mutations. Under mosaics are placed animals having different parts of the body different genetically and each part resembling a known character carried by the mother (with exception of orange). All other anomalous individuals are classed as freaks.

As pointed out above Habrobracon is especially suited to the finding of recessive mutations on account of male haploidy. Males would be likely to show genic changes at once whether the new gene had been present in the egg or had occurred in any early stage of development. Females on account of their diploid nature would be much less likely to show mutations.

Among directly treated animals abnormal types found were equally divided between the two sexes. If the abnormal females owed their anomalous characters to somatic mutations they must have been dominant muta-

tions unless one of the other improbable alternatives is used as explanation.

It has been shown in Drosophila (PATTERSON 1928) that when undoubted somatic mutations occur they involve but a small part of the animal and one character only, even when larvae are treated at an early stage. In many cases the non-inherited abnormalities in Habrobracon were extensive. For example, a female treated as a four day larva (almost ready for pupation) shows but one antenna, all six legs deformed, median ocellus small, and sting abnormal. It would be difficult to credit this wide range of change to somatic mutation without supposing that ancestral cells in head, thorax, and posterior end of abdomen had all mutated. Since the individual was a female these mutations would have had to be dominants or to have occurred simultaneously with the mutation or destruction of the normal allelomorphs. It is not difficult to suppose that regions of rapidly developing tissue may be directly injured by irradiation and that such injury, although not serious enough to cause death, would result in abnormal development even though chromosomes might in no way be involved.

Many of the types of abnormalities found in treated have been found many times in normal stock, tested dozens of times, and found to be non-inheritable. Abnormal abdomen is one of these, also one-eyed forms, abnormal antennae, etc.

It was expected in view of Doctor PATTERSON'S work (PATTERSON 1928) that mosaics might be found among animals directly treated. Thus males or heterozygous females might show areas of ivory or reduced or both if normal allelomorphs to these factors should mutate in somatic cells of larvae. No such mosaics were found. Black has mutated to ivory only once in all the work done on Habrobracon and type to reduced but once so that somatic mutations in these loci would not be frequent in all probability. It is also possible that a few ivory facets would be very difficult to identify for in black-ivory or black-orange mosaic eyes the facets between the two areas are dark and cloudy in appearance. Mosaics of cantaloup and non-cantaloup, involving another locus, show clear cut line of demarcation and this indicates that the cantaloup factor will be a good one for the study of this problem if, in addition to its visibility, it is found to mutate occasionally.

It was thought at first that the extensive shot condition found in a high percentage of heterozygous females and biparental brothers might be a result of somatic mutation of type to reduced or destruction of type-bearing chromosome. Since shot usually appeared in both wings and increased in extent and percentage with strength of treatment and age of larvae this

idea was given up. It seems best to consider it a developmental response to irradiation which differs in different genetic strains.

The mosaic males found among sons of treated females seem to the authors to be due to egg binuclearity without a doubt. The best argument for this is that they have never occurred in pure stocks. If a male with mosaic eyes or wings is produced by a heterozygous mother it is theoretically possible to explain it by somatic mutation from one eye color or wing form to the other in the haploid larva. If this were the case it should occur among sons of pure stocks also. Over 150 such mosaics have been found and every one was produced by a heterozygous mother.

A curious fact is that mosaic males from type-ivory mothers almost always have the light areas of the eyes orange in color instead of ivory. This was thought at first to be due merely to physiological interaction in the mosaic eye. Orange eyed males breeding as orange have since been produced by type-ivory mothers and this has led to the suggestion that ivory locus mutates to orange usually when associated with type. The fact that about 128 males with orange or partially orange eyes have been produced by heterozygous type-ivory mothers and not a single orange in tens of thousands of counts of homozygous ivory, and one only in addition to the original mutant in hundreds of thousands of type would seem to be significant. The males mosaic for eye color are often mosaic for reduced wing also when the mother carries that recessive factor but not otherwise. If somatic mutations are responsible for these masacis there must have been two mutations, and both, strangely enough, to the same recessive genes as those carried by the mother, or from those genes to the type alleiomorphs. There seems to be no reason why male mosaics due to somatic mutations not associated with egg binuclear.ty should not occur but until we get them produced by homozygous mothers as well as heterozygous we must hold to the binuclearity theory which, incidentally, explains adequately the numerous gynandromorphs found in Habrobracon.

Miss R. ELIZABETH CHALMERS (CHALMERS 1930) has shown that treatment of spermatogonia (adult males) has resulted in increase of mutation rate. Treatment of larvae seems to increase mutation rate slightly but to a less extent than treatment of adult males.

SUMMARY

1. Homozygous type females, type females heterozygous for ivory eye color and reduced wings, type males, ivory reduced males, and a few type biparental males possibly heterozygous for ivory and reduced, were irradiated as larvae while brothers and sisters were run as controls.

2. Treatments ranging from 730–4378 r units were given. No treatment had complete lethal or sterilizing effect, although the highest approached this.

3. Younger larvae were more susceptible than older and male larvae than female.

4. Irradiation tended to kill younger larvae immediately while older ones continued development and often died after metamorphosis but before eclosion.

5. Percentage of non-inherited abnormalites, "freaks," in directly treated individuals was significantly higher than in untreated stocks.

6. The high percentage of females among these freaks, extent of abnormalities, and their non-inheritance led to the conclusion that they were due to direct effects of irradiation rather than to mutation.

7. Many individuals treated as three and four day larvae showed wing veins disorganized, "shot," and resembling reduced to some extent.

8. Under treatment heterozygous females showed high percentage of extreme shot; biparental (supposedly heterozygous) males showed percentage and degree of shot similar to their heterozygous sisters; type females and males from stock number 31 showed low percentage of slightly shot; type females and males from stock number 1 showed high percentage of slightly shot.

9. Percentage and degree of shot within a group tended to increase with increased dosage.

10. No controls (brothers and sisters of treated) showed shot.

11. Shot appears to be due to physiological reaction to irradiation differing in different stocks rather than to mosaicism resulting from somatic mutation.

12. A very high percentage of females treated as larvae died without producing offspring, due apparently to weakness rather than to complete sterility.

13. Average number of progeny per fertile treated female was decidedly lower than per control sisters.

14. Eye and wing mosaic males appeared only among progeny of heterozygous females since they are due to binuclearity of egg.

15. Progeny of treated females showed higher percentage of non-inheritable abnormalities, mutations, and mosaics, than progeny of control sisters, but these percentages were not statistically significant.

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BEARING ON HEREDITY AND
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CORRIGENDA

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Page 423, line 5, for "II 6" read "IV 6."
Page 423, line 12, for "IV 13, IV 15" read "IV 14, IV 16."
Page 427, line 6, for "II (6)" read "II (4)."
Page 428, line 1, for "son" read "daughter."
Page 428, line 11, for "add myopia" read "and myopia."

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Page 8, footnote, for "$\frac{1}{e^{x^2/2^{\sigma^2}}}$" read "$\frac{1}{e^{x^2/2\sigma^2}}$."
Page 30, line 4 from bottom, for "55" read "45."
Page 34, line 10, for "w_l" read "w_1"
Page 41, line 10 from bottom, for "**58:**" read "**55:**"
Page 70, figure 5, for measurement letter "E" read "F"
Page 81, line 14 from bottom, for "the production of an amount of pollen" read "the production of an amount of bad pollen."
Page 83, lines 23 and 24, for "crossing over and so forth" read "and changes in chromosome structure."
Page 93, line 16, for "sterility of a diploid" read "fertility of a diploid."
Page 108, last line of text, for "P/P′′ " read "P′/P′′."
Page 120, last line, for "∂v" read "∂y."
Page 123, line 10, for "4Nn" read "4Nu."
Page 125, line 1, for "q" read "$\bar{q}$."
Page 126, line 12, for "q" read "$\bar{q}$."
Page 135, line 5 from bottom, for "y^{4Nsq}" read "e^{4Nsq}."
Page 141, lines 8 and 9, for "the mean gene frequencies are simply the ratios of the chances of fixation at each extreme, namely, $ve^{4Ns}/(u+ve^{4Ns})$" read "the mean gene frequency is simply the ratio of fixation in the favored direction to total fixation."
Page 193, line 2 from bottom, for "$1_{8II}+6_I$" read "$18_{II}+6_I$."
Page 348, line 9 from bottom, for "OEHLKERS, Fr., 1921" read "RENNER, O., 1921."
Page 364, line 3, for "y" read "γ."
Page 373, line 6, for "gametic" read "zygotic."
Page 474, line 4 from bottom, for "lagging at first metaphase" read "lagging at first anaphase."
Page 491, line 11, for "e_p" read "e_y."
Page 492, line 3 from bottom, for "or p_r" read "of p_r."

ERWIN BAUR

(FRONTISPIECE)

Professor Doctor ERWIN BAUR, Director of the INSTITUT FÜR VERERBUNGSFORSCHUNG at Berlin-Dahlem, and of the KAISER-WILHELM INSTITUT FÜR ZÜCHTUNGSFORSCHUNG at Müncheberg, Germany, was born at Ichenheim, Baden, April 16, 1875. He received his higher education in the Universities of Heidelberg, Freiburg, Strassburg and Kiel. In 1900 he passed the state examination in medicine at KIEL UNIVERSITY, and became for a short period a practicing physician, shipping on one occasion to Buenos Aires, as a ship's physician.

Turning soon completely to purely biological interests, he became in 1904 Privatdozent of Botany at the UNIVERSITY OF BERLIN, and in 1910 Associate Professor. In 1911 he was called to the LANDWIRTSCHAFTLICHE HOCHSCHULE in Berlin as full Professor of Botany, as successor to Geheimrat Professor Doctor L. KNY. In 1913 a new chair was established for him as Professor of Genetics in the LANDWIRTSCHAFTLICHE HOCHSCHULE, and a new Institution for this discipline was decided upon. This institution was first provisionally established at Potsdam. In 1921 the erection of the permanent INSTITUT FÜR VERERBUNGSFORSCHUNG was begun at Berlin-Dahlem. In 1927, largely through his influence, the KAISER-WILHELM INSTITUT for the Promotion of the Sciences, decided on the erection of its own great Institute for the study of breeding problems, especially in relation to their practical applications. This new INSTITUT FÜR ZÜCHTUNGSFORSCHUNG at Müncheberg, planned and developed by BAUR, was opened in the autumn of 1928. It is one of the greatest institutions of its kind in the world, having over 850 acres of arable land, accommodating about 30 investigators, and employing a large number of technical assistants.

In 1914 Baur was appointed Exchange Professor at the UNIVERSITY OF WISCONSIN, and had already embarked for the voyage to America by way of the Suez Canal and the Pacific Ocean, when the outbreak of the World War resulted in his immediate recall by his Government.

In addition to his extensive and comprehensive investigations in plant and animal genetics, BAUR has laid his fellow geneticists under a great indebtedness by founding and editing the "*Zeitschrift für induktive Abstammungs- und Vererbungslehre*," which was begun in 1909, and which has already run to 59 large volumes. This journal has provided one of the swiftest and most satisfactory means of publication available to writers of fundamental contributions in the field of genetics. For more extensive contributions he has established the "*Bibliotheca Genetica*" and in the field of applied genetics "*Der Züchter*." He is Associate Editor also of the "*Zeitschrift für Pflanzenzüchtung*," "*Fortschritte der Biologie*" and "*Gartenbauwissenschaft*." His textbook, "*Einführung in die experimentelle Vererbungslehre*," one of the best of the earlier genetical textbooks, has been repeatedly revised and republished. "*Die wissenschaftliche Grundlagen der Pflanzenzüchtung*" has been translated into Spanish and published in Buenos Aires. "*Menschliche Vererbungslehre und Rassenhygiene*" by BAUR-FISCHER-LENZ, has also appeared in several editions and has been translated into Swedish and English.

Doctor BAUR is an effective and inspiring speaker and has lectured by invitation in many foreign universities, including Lund, Stockholm, Upsala, Groningen, Leyden, Utrecht, Agram, Constantinople, Lisbon, and Coimbra.

He has also been the recipient of many academic honors, including the Rudolf Virchow medal and the Erzherzog Rainer medal. He is a Corresponding Member or Honorary Member of a long series of scientific academies and societies, both in Germany and abroad.

As President of the Organization Committee of the FIFTH INTERNATIONAL CONGRESS OF GENETICS, he opened that Congress, and was in a large measure responsible for its great success.

In the interest of his genetical and botanical experience he has traveled extensively in Asia Minor, in Spain and in South America.

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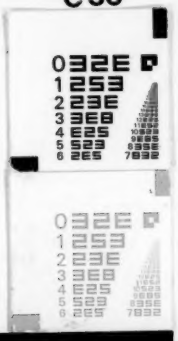
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